The effects of forest degradation on trophic interactions and elemental fluxes in an experimental landscape, Malaysian Borneo

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Degree of Doctor of Philosophy

Victoria Ann Kemp

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Details of collaboration and publications

Author contributions and additional collaborators are listed below for each chapter. This work was supported by the Natural Environment Research Council (NE/K016148/1).

- **Chapter 1:** Victoria Kemp wrote the chapter

- **Chapter 2:** Victoria Kemp, David Hemprich-Bennett and Matthew Struebig collected the data. VK performed the statistical analysis and wrote the chapter.

- **Chapter 3:** Victoria Kemp, Pavel Kratina, Jon Grey, Stephen Rossiter and Owen Lewis designed the study and wrote the paper. Victoria Kemp and David Hemprich-Bennett collected the data, and VK analysed the samples. VK performed the statistical analysis.

- **Chapter 4:** Victoria Kemp, Pavel Kratina, Jon Grey, Stephen Rossiter and Owen Lewis designed the study. VK and PK wrote the paper. Victoria Kemp and David Hemprich-Bennett collected the biological data, and David Coomes, David Milodowski and Tom Swinfield collected and processed the remote-sensed environmental data. VK analysed the biological samples and performed the statistical analysis.

- **Chapter 5:** Victoria Kemp, Pavel Kratina, Jon Grey and Eleanor Slade designed the study and wrote the paper. VK and ES collected the data. VK analysed the biological samples and performed the statistical analysis.

- **Chapter 6:** Victoria Kemp wrote the chapter

“What escapes the eye…

is a much more insidious kind of extinction:

the extinction of ecological interactions”

(Dan Janzen, 1974)

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ABSTRACT

Despite occupying only 12% of Earth's surface, tropical forests contain disproportionate biodiversity, contribute approximately 40% of terrestrial net primary productivity, and contain 20% of global carbon biomass. In parallel, tropical forests experience extreme destruction and degradation, leading to a pressing need to understand the value of degraded forest. Recent work suggests that degraded forests which retain a high percentage of native tree cover, or are in late stage recovery, can support levels of species richness close to those of intact forests. However, the impacts of tropical forest degradation on ecosystem functions remain unclear due to a paucity of studies. Among the key functions that may be modified by habitat degradation is the flux of energy and nutrients through an ecosystem. In chapter two, I determined insectivorous bat community response to short- and long-term pressures, climatic and logging respectively. In the second and third chapters. In the third and fourth chapters I examined how forest degradation influenced bat resource use, food web structure, and associated ecological functions. I focused on summarising complex interactions between bats, their prey and basal resources by analysing naturally abundant isotope compositions. Initially, I focused on shifts across a narrow degradation gradient, and found that both landscape- and local-scale traits correlated with changes to isotopic niche and trophic position, respectively. I extended this investigation to examine patterns across both logged and primary forest, and examined how long term habitat changes correlated with dietary shift. Furthermore, I explored how short-term environmental stress interacted with established gradients of habitat quality. In the last chapter, I undertook a ^{15}nitrogen-tracer mesocosms study to investigate dung beetle effects upon nitrogen cycling in tropical soils, facilitating future studies on the response of nitrogen processes to environmental change. This research assists in identification of landscape elements which should be favoured by management policies in order to retain ecosystem functioning.

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CHAPTER 1

General Introduction

Maliau Basin Conservation Area

Tropical biodiversity

Diversity of living organisms is distributed non-randomly across the globe and the overwhelming majority of biodiversity is found in the tropics (Barlow *et al.* 2018). Tropical ecosystems provide myriad critical goods and services to the World's poorest communities (Bradshaw *et al.* 2009; Cardinale *et al.* 2012), as well as globally important ecosystem services including sources of new medicines and climate regulation (Foley *et al.* 2007). Humid tropical forests cover less than 12% of the Earth's ice-free land surface, yet are responsible for 25% of carbon storage and 33% of net primary productivity (Bonan 2008), and have a critical role in Earth's nutrient cycles (Townsend *et al.* 2011). That our planet is facing rapid decline in biodiversity is no longer in question, with negative effects for ecosystem stability (McCann 2000; MacDougall *et al.* 2013), and healthy functioning (Lodge *et al.* 2005). There are a multitude of local pressures leading to biodiversity losses including pollution of ecosystems, overexploitation of resources therein, invasion and dominance by non-native taxa, as well as global stressors such as climate change. However, it is habitat loss and degradation which represent the leading threats to global biodiversity (Hanski 2011; McRae *et al.* 2014), and on current trajectories, biodiversity targets to reduce loss of natural habitat will not be met by 2020 (Tittensor *et al.* 2014). The highest rates of forest conversion are in the tropics (Pereira *et al.* 2012) caused primarily by timber extraction and agricultural expansion (Foley *et al.* 2005; Laurance *et al.* 2014; FAO 2018), and show no signs of abating (Hansen *et al.* 2013; Potapov *et al.* 2017; Hughes 2018). Tropical biodiversity is more vulnerable to habitat loss and degradation than temperate species due to life history traits such as dispersal limitation and sensitivity to climatic fluctuations (Edwards *et al.* 2014a). High rates of habitat change in tropical ecosystems, and high species vulnerability to those changes has resulted in high extinction rates for tropical species. For example, 85 % of recorded vertebrate extinctions include tropical species (Barlow *et al.* 2018). Thus, it is critical to understand trajectories of tropical forest degradation in order to predict and mitigate those changes to complex networks of interactions associated with simplification of communities.

Local threats to biodiversity: logging, fragmentation and agricultural conversion

Extraction of valuable timber is pervasive in tropical forest ecosystems. One fifth of forests have been selectively logged at some level from 2000 to 2005 (Asner *et al.* 2009), making primary tropical forest increasingly rare. Small-scale fragmentation of the forest understorey by roads and other logging-associated features, cause negative impacts associated with habitat edges such as increased tree mortality (Broadbent *et al.* 2008). Gaps in canopy cover following logging, *i.e.* from extracted and dying trees, expose the forest floor and alter environmental conditions such as temperature, humidity and soil moisture (Hardwick *et al.* 2015). Regenerating logged forests tend to have reduced structural complexity compared to their old-growth counterparts (Okuda *et al.* 2003; Asner *et al.* 2009), with potentially negative consequences for multiple ecological parameters such as habitat diversity (Tews *et al.* 2004) and heterogeneity (Kitching *et al.* 2013). There is strong indication that overall floral and faunal biodiversity is reduced in regenerating logged forest compared to old-growth forest (Meijaard *et al.* 2006; Gibson *et al.* 2011), although there is much inconsistency between taxonomic groups (Newbold *et al.* 2014) and spatial scales (Berry *et al.* 2008) for examples. Altered environmental conditions and forest structure in regenerating forests influence key ecological processes governing nutrient cycling and productivity (Denslow 1987; Prescott 2002; Riutta *et al.* 2018).

However, land-use change from natural forest to agricultural land is widely considered the more dangerous threat for biodiversity and ecosystem functions of tropical forests (Sala *et al.* 2000; Sodhi *et al.* 2004), causing direct habitat loss at the local scale and indirect degradation at the landscape scale (Villard & Metzger 2014). This century the human population is predicted to reach 11 billion, which in conjunction with increased per-capita consumption will require large increases in food resources (United Nations 2013). Thus, major expansion and intensification of agricultural practices in tropical landscapes is expected, with accompanying loss and alteration of both old-growth and regenerating forests (Laurance *et al.* 2014). This will add to the substantial proportion of the World's remaining tropical forest which already exists as patches embedded in agricultural landscapes (Malhi *et al.* 2014), and thus exposed to fragmentation effects. Loss of forest through conversion to agricultural land has consistent, negative effects upon biodiversity (Villard & Metzger 2014). Furthermore, the breaking apart of remnant forest delivers additional challenges to biodiversity and functioning, linked to but independent of loss of habitat: the creation of habitat edges (Ewers & Didham 2006); reduction in habitat area (Lawton 1999); and isolation from other areas of suitable habitat (MacArthur & Wilson 1967).

South East Asian island of Borneo

The diverse island of Borneo, Malaysia suffers some of the highest timber extraction rates in the world (Fisher *et al.* 2011), owing to forest dominance by commercially valuable dipterocarp species. Moreover, the rapid expansion of African oil-palm (*Elaeis guineensis*) plantations, as in much of South East Asia, has led to high levels of deforestation and landscape degradation (Gaveau *et al.* 2016). Forested land provides a cheap option for conversion to oil palm due to the demand for native species from the timber industry (Fitzherbert *et al.* 2008). Financial incentivisation, combined with minimal insurance from international policies that oil palm expansion is diverted away from natural forests, makes degraded forests highly vulnerable to conversion (Gibbs *et* *al.* 2010). Given the destructive effects of oil palm expansion at the local and landscape level, there is increasing urgency to understand the conservation value of relatively unprotected, regenerating forest (Edwards *et al.* 2014b; Gardner *et al.* 2014). Of the remaining forest on Borneo, close to half has been logged (Gaveau *et al.* 2014), and substantial areas have experienced high-intensity logging of multiple rounds (Bryan *et al.* 2013).

The value of degraded forests

Although biodiversity is generally lower in logged forest than in old-growth forest (Gibson *et al.* 2011), the number, intensity and extent of past logging are major factors in determining the degradation of forests in terms of biotic composition, and forest structure and function (Banks-Leite *et al.* 2014; Bicknell *et al.* 2014; Malhi *et al.* 2014). The effects of logging on species richness can be minimal, with logged forests hosting up to 75 % of primary forest diversity (Putz *et al.* 2012), even following multiple logging cycles (Edwards *et al.* 2011). Specifically, species diversity in logged forest increases with reduced intensity of tree extraction (Banks-Leite *et al.*, 2014) and proximity to old-growth forest (Dent & Wright 2009). A major challenge for future policy and forest management is to understand the conservation value of regenerating forests with different logging histories (Melo *et al.* 2013).

Post-logging impacts on the forest ecosystems may be more pervasive, and yet more subtle, than alteration to classic community metrics such as species richness. Until recently the extent to which habitat degradation influences ecosystem functions had received little attention (Lewis 2009; Hector *et al.* 2011; De Coster *et al.* 2015). Studies have now begun to examine the effects of habitat modification on the functional and phylogenetic diversity dimension (Chapman *et al.* 2018). However, there remain calls for studies of anthropogenic impacts to move beyond assessments of species richness and to incorporate information on biotic interactions, and associated ecosystem functions (Antiqueira *et al.* 2017; Barnes *et al.* 2017). Ecosystem functioning includes multiple ecosystem processes controlling fluxes of energy, nutrients and organic matter through an ecological system (Cardinale *et al.* 2012). Such processes include primary production, element cycling, food web dynamics, resource use and trophic energy transfers.

Oil palm plantations

In oil palm plantations, abiotic and biotic processes are fundamentally altered compared to forest. These changes include highly simplified vegetation structure, increased diurnal temperatures and decreased humidity (Fitzherbert *et al.* 2008). As a result plantations support a decreased species richness in a wide number of studied taxa compared to old-growth or regenerating forest (Turner *et al.* 2011), and altered community composition (Fayle *et al.* 2010). In oil palm plantations, reduction in tree species richness and associated architectural simplification are inevitable. However, these systems retain significant structural complexity especially compared with other agricultural crops (*e.g*. soya bean or rice; Foster *et al.* 2011). Understanding the intensity of the conversion process upon biotic communities has focused upon retention of ecosystem health at the landscape level (Edwards *et al.* 2010). However, conservation of ecosystem processes within oil palm habitat is an important and currently neglected area of research (Foster *et al.* 2011). Key ecosystem processes to be monitored in oil palm plantations include biocontrol, pollination, and soil fertility, for examples. Thus, there is a major challenge to increase understanding of how forest conversion affects ecosystem functioning at local as well as landscape scales.

Ecosystem functioning in modified habitats and stable isotopes

Among the key ecosystem functions that may be modified by habitat degradation is the flux of energy and nutrients (Cardinale *et al.* 2012; Barnes *et al.* 2017). Modifications to functioning in degraded landscapes may result from altered trophic structure, arising from changes to species interactions (Estes *et al.* 2011). Predators may respond to habitat change, and associated changes to prey composition, in a manner that fundamentally alters trophic structure and energy pathways throughout ecosystems (Tunney *et al.* 2014; Antiqueira *et al.* 2017), with far-reaching ramifications for healthy ecosystem functioning (Duffy 2003; Estes *et al.* 2011; Atwood *et al.* 2013). Similarly, changes in the resource base may propagate through the food web with consequences for density, abundance and community composition of consumers (Chen & Wise 1999). The detailed analysis of both top-down and bottom-up processes offer very powerful tools for the prediction of habitat modification upon whole ecosystems. Closely linked, nutrient cycling is important in regulating primary productivity in many ecosystems (Pajares & Bohannan 2016), especially in the often nutrient-limited tropics (Swift *et al.* 1998). However, the response of processes regulating nutrient cycling to land-use changes is still in its infancy, and there are calls to better understand the maintenance of healthy functioning in conversion landscapes (Lewis 2009; Foster *et al.* 2011; Dislich *et al.* 2017).

Stable isotope analyses (SIA) can be used to track pathways by which a chemical substance moves through the biotic and abiotic components of ecosystems. These analyses quantify and compare the ratio of naturally occurring isotopes of a particular chemical, which changes due to distinct physical behaviours of the two isotopes in their environment. Elements of particular interest in a changing environment are those that cycle most tightly with organic matter, *i.e.* C, N, H, O and S (Fry 2008). Similar applications can involve isotope-tracer studies, whereby compounds labelled with heavy, naturally rare isotopes (*i.e.* ^{13}C or ^{15}N) are traced through ecosystems. Both approaches can determine where plants and animals derive their resources from (Barraclough 1991; Gannes *et al.* 1998), and thus reveal changes to the cycling of energy and nutrients through an ecosystem. Natural abundance studies of carbon and nitrogen isotope ratios, have been widely used in the analyses of food web structure and dynamics (Fry 2008). Ratios of nitrogen stable isotopes ($\delta^{15}N$) exhibit dependable stepwise trophic enrichment (~3.4‰), thereby providing reliable indicators of consumer trophic position relative to known basal resources (Gannes *et al.* 1998; Post 2002b). Ratios of carbon stable isotopes ($\delta^{13}C$) are enriched minimally with trophic transfer, but vary substantially across different basal resources, and are therefore a good indication of resource use (DeNiro & Epstein 1978; Newsome *et al.* 2007). In comparison, isotope-tracer studies measure units of change in isotope ratio above natural levels of enrichment that occur with ecological interactions. Isotope-tracer studies have improved our understanding of nutrient cycling in soil, plants, and food webs (Barraclough 1991; Ngai & Srivastava 2006; Nervo *et al.* 2017).

Natural abundance of $\delta^{13}C$ values can reveal divergent foraging strategies, for example shifts in resource base from C_3 to C_3/C_4 plants (Sullivan *et al.* 2006), or understorey to canopy trees (Crowley *et al.* 2013). Useful applications have included the study of dietary specialisation (Fry *et al.* 1978), herbivore diet shifts from dominant, native plants to agricultural crops (Mizutani *et al.* 1992) and resource partitioning by sympatric species (Crowley *et al.* 2013). In compliment, study of natural abundance $\delta^{15}N$ values can reveal changes in relative trophic position of individuals or species following subtle changes in food webs (*e.g.* Vander Zanden *et al.* 1999; Tunney *et al.* 2014). Stable isotopes provide a continuous measure of trophic position that allows capture of the complex interactions and trophic omnivory prevalent across ecosystems (Post 2002b; Thompson *et al.* 2007).

Isotopic bi-plots (*i.e.* $\delta^{13}C$ versus $\delta^{15}N$) represent multivariate space comparable to the widely applied n-dimensional ecological niche, because an animal's isotopic signature is directly influenced by what it consumes as well as the environment in which it lives (Hutchinson 1978; Newsome et al. 2007; Ben-David & Flaherty 2012). Thus, stable isotopes allow for coarse description of often complex and cryptic species interactions (Polis & Strong 1996; Nielsen et al. 2018), and provide a means to relate abiotic factors to an organism's ecological role (Layman *et al.* 2007b). Stable isotope values of representative individuals can determine the ecological (isotopic) niche of a species or functional group (Bearhop et al. 2004). Given that the an organisms' isotopic niche space implies its resource use, changes to niche parameters can reveal changes to interspecific (Matich et al. 2016) and intraspecific (Wood et al. 2017) competition as well as degree of dietary specialisation (Broders et al. 2014), prey abundance (Jiménez *et al.* 2017) and resource access (Layman *et al.* 2007b). Most notably, quantifying changes to isotopic niche parameters is of high value to understanding the diverse effects of human activities upon species and communities (Newsome et al. 2007). The axes of a species' isotopic niche are sensitive to habitat fragmentation (Layman *et al.* 2007b) and other environmental stressors (Reddin et al. 2016).

Advantages and disadvantages of stable isotopes

Stable isotope analysis (SIA) is a powerful tool to study the ecological interactions of flora and fauna across disparate ecosystems. Many applications of SIA have aimed to characterise consumer diet, generating quantitative and continuously distributed variable, with statistical handling much improved compared to classic diet tracing methods such as morphological faecal analyses (Nielsen et al. 2018). Stable isotopes also offer space-and time-integrated overview of the composition of the diet of an individual, population or community (Fry 2008) as opposed to morphological and more recently molecular (Clare *et al.* 2009) faecal analyses, by which diet composition reflects diet over a short time-span preceding sampling. These properties have improved insights into human-driven shifts in community structure (Layman *et al.* 2007b; Schmidt *et al.* 2007), dietary contributions (Parnell *et al.* 2013), and patterns of isotopic niche variation (Layman *et al.* 2007b; Semmens *et al.* 2009; Jackson *et al.* 2011; Cucherousset & Villéger 2015). However, there is considerable simplification of the dynamics of isotopic incorporation into animal tissues, potentially causing inaccuracies in the interpretation of isotopic signatures (Martinez del Rio *et al.* 2009; Ramos & González-Solís 2012; Nielsen *et al.* 2018). Heavy isotopes are known to increase up the food chain, however factors determining the degree of biomagnification are poorly understood, and unaccounted for can lead to misinterpretation of patterns over time and space (Martinez del Rio *et al.* 2009). For example, the trophic enrichment factor for ratios of nitrogen, ($\Delta\delta^{15}N$), has been shown to change with nutritional status (Voigt & Matt 2004; Gorokhova 2017), and for carbon ($\Delta\delta^{13}C$) are affected by the relative proportion of animal and plant material in the diet (McMahon *et al.* 2010). Isotope-tracer studies are far less sensitive to misinterpretation of ecological and behavioural characteristics associated with unresolved dynamics of isotopic incorporation.

Diversity and diet of tropical bats

Bats are the most ecologically diverse mammals in the tropics (Dammhahn & Goodman 2013) and are characterized by high local abundance; species richness, and trophic diversity, representing distinct major feeding guilds (Kalka & Kalko 2006). However, bats are highly susceptible to the effects of human disturbance given their low reproductive rate, longevity and high metabolic rates (Voigt & Kingston 2015). In the study of tropical bats, and their responses to human disturbance, assemblages in the Neotropics have been much better described than their Old World counterparts. These two groups are considerably distinct, given that they are dominated by different families, and thus their responses to disturbance are likely to be somewhat divergent. In the Neotropics there is evidence for declines in species richness and abundance in degraded forests (Medellín *et al.* 2000; Peters *et al.* 2006), but as with many animal taxa, inconsistent responses are found between different functional guilds (Martins *et al.* 2017) and impacts are diminished under less intense extraction methods (Bicknell *et al.* 2014). From the more limited studies in the Old World, there is evidence that bat species composition is sensitive to reduction in canopy closure and height as well as roost availability (Struebig *et al.* 2013). In line with multi-taxa studies assessing conservation value (*e.g.* Gibson *et al.* 2011) regenerating forest appears to be an important repository for bat biodiversity, conserving a subset of primary forest species richness (Meyer *et al.* 2015).

Despite recent advances in understanding how tropical bats respond to habitat disturbance, few studies assess the effects of disturbance upon their ability to provide key ecosystem services (Meyer *et al.* 2015). Bats provide numerous ecosystem services critical for healthy ecosystems (*e.g.* insect suppression, nutrient repollination, and seed dispersal; Kunz *et al.* 2011). Specifically, insectivorous ensembles have been shown to supress herbivorous insect populations in rainforests (Kalka *et al.* 2008) as well as agricultural landscapes (Denmead *et al.* 2017). Numerous studies show an associated increase in crop yield with bat-mediated decrease in insect abundance, however intraguild predation (consumption of both intermediate predators and herbivores) can lead to the opposite effect (Maas *et al.* 2016). Old World insectivores largely comprise of species either foraging on the wing, ‘aerial insectivores’, or taking them from vegetation surfaces, ‘gleaning insectivores’ (Kalka & Kalko 2006), and consume a wide range of different insect orders (Kunz *et al.* 2011). Bat diet often incorporates distinct resource compartments (“multichannel feeders”; Wolkovich *et al.* 2014), which may have stabilizing effects on food webs (Rooney *et al.* 2006). As highly mobile predators, pursuing areas of concentrated prey source (Wickramasinghe *et al.* 2004; Kalcounis-Rueppell *et al.* 2007), bats are likely to reflect both local and landscape-scale logging impacts in their behaviour and diet composition. The behavioural responses of mobile, multichannel feeders to changes in their environment (*e.g.* habitat connectivity; LeCraw *et al.* 2014) can cause disproportionate changes to food web dynamics and stability (McCann *et al.* 2005; Bartley *et al.* 2018). Resource use can also be impacted by indirect effects of habitat change that alter prey availability. Degraded forests host distinct insect communities to old-growth forest with reduced species richness, and showing homogenisation of species composition and shifts in trophic structure driven by idiosyncratic responses of different taxa to altered biotic and abiotic conditions (Lawton *et al.* 1998; Barlow *et al.* 2007; Tylianakis *et al.* 2008). Changes to insect communities are likely driven by a combination of top-down control (Kalka & Kalko 2006) and bottom-up processes (*e.g.* plant-hosts available locally to larvae; Kitching *et al.* 2013).

Dung beetles as models for biodiversity and ecosystem functioning

Nutrient cycling is an important ecosystem function, and a focus of research in disturbed habitats (Swift *et al.* 1998; Lavelle *et al.* 2005), including shifts in regulatory processes between natural and agricultural ecosystems (Tscharntke *et al.* 2012). Given that large areas of logged forest and agriculture will be key features of future tropical landscapes, it is essential to better understand the maintenance of ecosystem functions in these ecosystems (Foster *et al.* 2011). Decomposition is a key component in the cycling of nutrients when we consider that up to 90% of global terrestrial plant production can be channelled through the dead organic matter pool (Cebrian 1999). There is a growing body of research investigating how altered biodiversity of decomposers affects rates of decomposition processes in temperate aquatic and terrestrial systems (Gessner *et al.* 2010), but there remains a large knowledge gap in tropical ecosystems. It is generally considered that decomposer communities are affected by conversion from forest to oil palm (Fayle *et al.* 2010; Turner *et al.* 2011), but there is currently little evidence as to how these changes may alter decomposition and soil fertility (Foster *et al.* 2011). Dung beetles (Coleoptera: Scarabaeoidea) are a specialist component of the soil macrofauna, and represent an ideal model group for exploring the relationships between biodiversity and ecosystem functioning because they act as important nutrient recyclers and their diversity and function are sensitive to land-use (Nichols et al. 2008). However, the effects of dung beetle activity on decomposition processes, and their role in soil fertility and plant-available nutrients remain poorly understood (*e.g.* Beynon et al. 2015). Owing to the increasing focus on dung beetle ecology (Nichols *et al.* 2008) and in particular the provision of ecosystem functions and services (Beynon *et al.* 2015), this group offers a powerful tool to further investigate the role of decomposers in the health of tropical soils.

Conservation perspective

The prevalence of logging activities in the tropics (Gaveau *et al.* 2014), combined with the increased susceptibility of logged forest to future conversion processes (Gibbs *et al.* 2010), necessitates protection of degraded forest. In order to increase protection through land management policy it is critical to improve our understanding of how logging history and the landscape context of areas of degraded forest affect their conservation value (Malhi *et al.* 2014). The importance of tropical forest for supporting biodiversity and carbon storage is recognised via numerous local, regional and international conservation policies. For example, the United Nations developed the

Reduced Emission from Deforestation and Degradation+ programme (REDD+) in order to mitigate the detrimental effects of carbon emissions following clearing and degradation of natural forest (United Nations 2018). This programme references the sustainable management of forests and promotion of biodiversity conservation, providing an opportunity to safeguard areas of degraded tropical forest high in both carbon and biodiversity (Paoli *et al.* 2010). Indeed, it has been increasingly recognised that improvements in the management of degraded forest can be facilitated by synergistic interaction between initiatives (Putz *et al.* 2012). In parallel, there is an emerging focus on the potential of non-forested land uses, *i.e.* agricultural areas to maintain ecosystem functioning locally rather than solely depending on natural habitat in the surrounding area. Our increased understanding of ecosystem processes in palm oil plantations could inform future management policies to make them more biodiversity friendly, especially given existing frameworks such as the Round Table on Sustainable Palm Oil (www. rspo.org).

The SAFE project

The Stability of Altered Forest Ecosystems (SAFE) project (Ewers *et al.* 2011) in Sabah, Malaysian Borneo is one of the World's largest ecological experiments. The SAFE project encompasses 7200 Ha of lowland dipterocarp rainforest in the Kalabakan Forest Reserve (N4.728, E117.596; Fig. 1.1). The embedded experimental area includes large areas of selectively logged forest, the majority of which is destined for conversion to oil palm plantation, leaving dispersed remnant forest patches. Thus, the landscape is characteristic of land-use trajectories common across much of Southeast Asia (Fitzherbert *et al.* 2008; Gaveau *et al.* 2014) and increasingly other parts of the tropics (FAO 2018). The SAFE project aims to explore ecological changes in human-modified habitat with particular focus on changes across gradients of degradation, and whether spatial context can mitigate or exacerbate impacts of localised changes to forest structure. The SAFE landscape provided a pre-conversion gradient of logging disturbance: logged forest sites had been exposed to at least two rounds of extraction, with additional logging rounds in the experimental area destined for conversion to oil palm plantation. Additional logging had resulted in a range of forest cover, including substantial areas which were entirely devoid. In comparison, the logged forest site 'LFE' was only twice-logged and all logging ceased in the 1990s, allowing recovery in the intervening decades to tall forest with minimal gaps in the canopy. The area to the south of the SAFE project had been established as oil palm concessions, some of these concessions since several decades ago.

I conducted much of my research in the SAFE experimental area, and also surveyed two primary forest sites within the greater SAFE landscape: the Danum Valley conservation area (DVCA; N4.962°, E117.689°) and Maliau Basin conservation area (MBCA; N4.853°, E116.844°), located 36 km north and 69 km west of the SAFE project, respectively (Fig. 1.1; Table 1.1). DVCA is a 438 km^2 lowland dipterocarp forest reserve close to the Segama River at 210 m elevation. In comparison, MBCA is a 588 km^2 lowland and hill dipterocarp forest reserve, close to the Maliau River and reaching 1, 675 m at the highest point. Both are afforded the highest status as Class I Protected Forest Reserves by the Sabah state government, owing to the value of the areas for conservation and education. See Table 1.2 for classification of all sample sites. To investigate nutrient cycling in tropical soils, I also performed a dual-habitat study in both high-quality logged forest in SAFE (site LFE) and nearby oil palm plantation (Fig. 1.1).

Logged forest sites within the SAFE experimental were located 2 to 7 km apart (Table 1.1). From mid-2015 sites in the experimental area were undergoing final selective harvest prior to conversion and were at the early stages of fragmentation. By the 2016 campaign, full fragmentation had occurred resulting in six isolated sample sites (B, C, D, E, F and LFE). By the 2016 campaign active disturbance had already ceased, and remained absent through to the end of this study. However, LFE remained contiguous with the Ulu Segama forest reserve to the north throughout the study period, and somewhat buffered from the landscape disturbance (see Table 1.3 for description of the habitat status of sites in each sample year). LFE is treated as a control for investigating ecological responses to emerging local pressures, *i.e.* active logging.

Climatic context

Severe droughts linked to El Niño occur roughly once every ten years (Malhi & Wright 2004). During our 2015 sampling campaign, South East Asia was experiencing the early stage of an El Niño event, with reduced rainfall. By the beginning of our 2016 campaign surface air temperatures surpasses national records (Thirumalai *et al.* 2017), and there was widespread drought across our sampling locations (VK personal observation). By 2017 the climate was returning to an ENSO-neutral state. These changes to climate may interact with habitat degradation (Côté *et al.* 2016), which represents further challenge for mitigating complex biotic responses (Barlow *et al.* 2018). For example, forest clearing can disrupt climate regulation, increase environmental temperature and intensify El Niño events, themselves associated with unusually hot and dry conditions compared to the long-term average (McAlpine *et al.* 2018). Considering more extreme ecological effects are predicted under future El Niño events, due to exacerbation by long-term warming (Thirumalai *et al.* 2017), understanding their synergistic ecological effects with local pressures such as habitat degradation is paramount for future management of tropical landscapes.

Objectives and chapter outlines

In this thesis, I used numerous ecological metrics in order to investigate the effects of anthropogenic change upon tropical terrestrial landscapes. I aimed to improve understanding of the conservation value of tropical logged forest by investigating the extent to which the diet of bats, high-level predators, was altered with implications for their capacity to provide key ecosystem services (ecosystem stability, biocontrol of insect prey). I explored the spatial scale at which structural heterogeneity was correlated with altered resource use, as well investigating temporal changes. In addition, I added to the minimal knowledge regarding the links between biodiversity and decomposition processes in tropical terrestrial ecosystems, and compared underlying dynamics in natural and human-dominated systems.

In chapter 2, I described the response of Old World tropical bat assemblages to a discrete gradient of forest degradation, from primary forest to repeatedly logged forest. I also investigated how assemblages changed over sampling years. The impetus for this analysis was to provide whose assemblage context for the findings in the subsequent two chapters, necessarily focusing only on abundant species. I found differences in all community metrics across sites, but only for species richness among years.

Understanding community change is a first step to inform the value of logged forest for conserving biodiversity. Beyond this, changes to community metrics, such as composition, are indicative of changes to community functioning. For examples, reductions in population densities of common species can substantially affect functional trait composition of communities (De Coster *et al.* 2015) and ecosystem function (Spaak *et al.* 2017). Insectivorous bats exert top-down control upon community structure and functioning, thereby giving particular importance to understanding changes to their populations. Changes to community composition can result from disparate effects of logging upon species (Cardillo *et al.* 2005; Thorn *et al.* 2018), and among individual functional guilds (Cleary *et al.* 2005; Manhoudt *et al.* 2007), owing to specific life-history traits. However, community metrics are a coarse measure of functional change as each species is not of the same functional value of another within a given community context. Looking at changes in diet can provide a clearer picture. In chapters 3 and 4 I focused on representative abundant bat species to investigate changes to resource use, applying SIA of natural abundance carbon and nitrogen isotope ratios. In chapter 3, I investigated changes to species' trophic position and isotopic niche over a relatively narrow gradient of quality of regenerating forest. I examined how spatial structure of a landscape can mediate or exacerbate the ecological impacts of logging. I found that habitat quality thresholds, below which we see substantial effects on trophic interactions and associated ecosystem functions, are higher than previously considered, owing to prior focus on classic community metrics.

In chapter 4, I shifted focus from the response of bat populations to whole bat assemblages, and deepened the understanding of mechanisms underlying consumer dietary shifts, by quantifying changes in the isotopic variation at lower trophic levels (*i.e.* insects and basal resources). Furthermore, I extended the analysis to consider a wider gradient, from primary forest to repeatedly-logged forest. I analysed three years of data to compare medium-term (multidecadal) responses with those over the shorter-term (1-2 years) in the context of El Niño, and explored interactive effects of logging and climate change at a given location and time. I found stronger interannual responses than expected, and of a similar direction and magnitude to those observed over a broad spatial gradient of habitat quality.

In chapter 5, I designed a novel method of isotope-tracer application to investigate nutrient cycling in tropical soil systems. I explored the role of dung beetle communities in availability of dung-derived nitrogen to aboveground biomass, and aimed to detect underlying ecosystem-specific nutrient dynamics (logged forest versus oil palm). Novel methods of isotope-tracer addition to soil systems and use of a model taxa with increasingly well-resolved ecology, provides a powerful pathway for studying the link between tropical biodiversity and ecosystem functioning, and local retention of the latter in areas of agricultural land use. I found evidence for differential nutrient cycling in forest and agricultural ecosystems, and differences in the rate of dung-derived nitrogen incorporation into the soil matrix, and assimilation by aboveground primary production, with and without dung beetles. My results are contrary to predictions from previous studies and current wisdom regarding the effect of dung beetles on nitrogen cycling, having found a negative relationship between dung beetle presence and the rate of nitrogen assimilation. This work both highlights of the need for further study in this area, as well as delivering a new method with clear ecological application for looking at whole system dynamics.

Finally, I consolidated my findings together in a general discussion. Here, I aimed to evaluate the use of natural abundance stable isotope analyses for detecting altered trophic interactions and food web structure over spatial and temporal gradients, as well as the use of isotope-tracer studies for elucidating more mechanistic changes.

Tables and Figures

Table 1.1. Distance (km) between each of the eight sample sites. Distances are calculated between site-specific mean harp trap locations, weighted by the number of bats caught at each trap location. The last row presents the sum total distance from one site to all other sampled sites.

	DVCA	MBCA	LFE	B	C	D	E	F
DVCA	**0**	95.71	34.56	33.07	34.54	36.66	38.68	41.37
MBCA	95.71	**0**	70.01	72.24	73.08	69.17	69.03	63.94
LFE	34.56	70.01	**0**	2.24	3.74	2.18	4.49	7.17
B	33.07	72.24	2.24	**0**	2.48	3.78	5.61	9.22
C	34.54	73.08	3.74	2.48	**0**	3.91	4.68	9.32
D	36.66	69.17	2.18	3.78	3.91	**0**	2.37	5.55
E	38.68	69.03	4.49	5.61	4.68	2.37	**0**	5.1
F	41.37	63.94	7.17	9.22	9.32	5.55	5.1	**0**
Total	314.59	513.19	124.39	128.64	131.74	123.61	129.96	141.67

Table 1.2. Current classification and logging history of all forest sites.

Site	Forest type	Logging history	Logging intensity
MBCA	Primary	None	None
DVCA	Primary	None	None
LFE	Regenerating	Twice-logged	Light logging
B	Regenerating	Repeatedly logged	Heavy logging
C	Regenerating	Repeatedly logged	Heavy logging
D	Regenerating	Repeatedly logged	Heavy logging
E	Regenerating	Repeatedly logged	Heavy logging
F	Regenerating	Repeatedly logged	Heavy logging

Table 1.3. Habitat status of sampling sites in those years they were sampled.

Site/ Disturbance	Primary forest	Recovering forest (twice-logged)	Recovering forest (at least twice-logged)	Fragmented forest
MBCA	2016, 2017	-	-	-
DVCA	2016, 2017	-	-	-
LFE	-	2015, 2016, 2017	-	-
B	-	-	2015	2016, 2017
C	-	-	2015	2016, 2017
D	-	-	2015	2016, 2017
E	-	-	2015	2016, 2017
F	-	-	-	2015

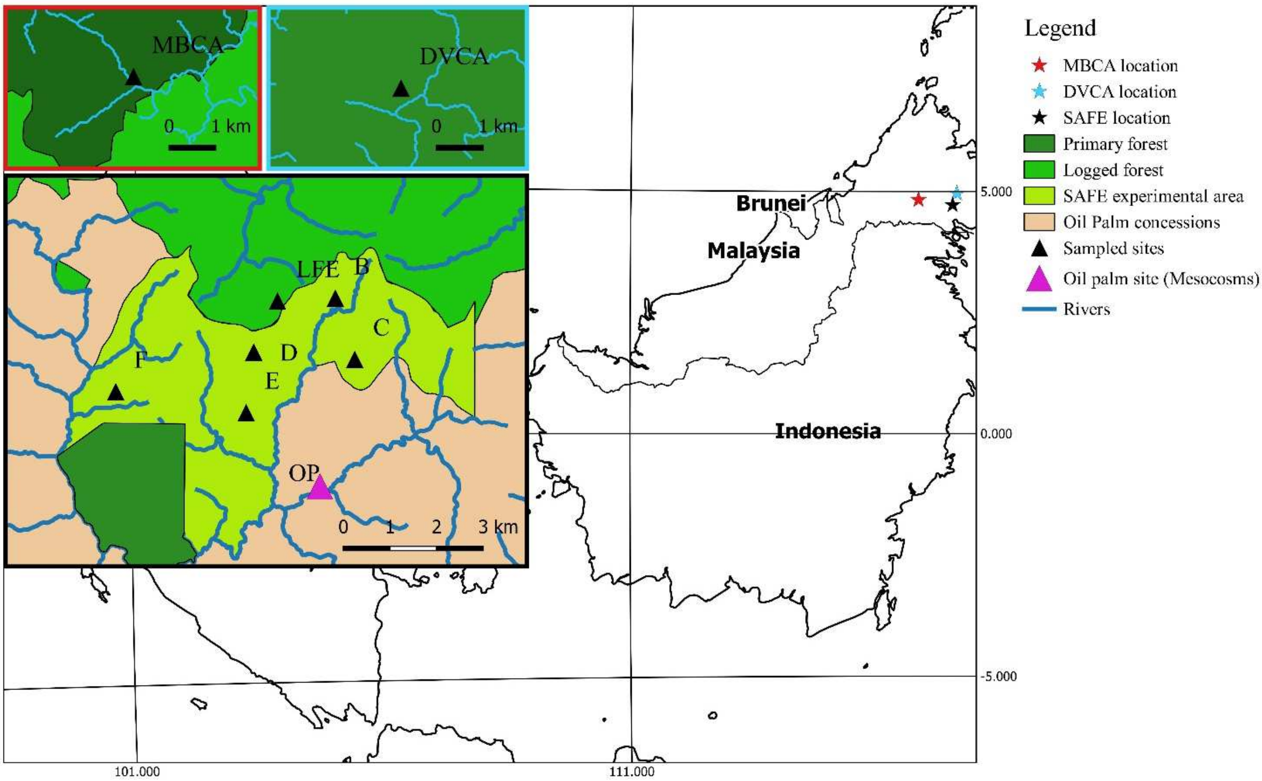


Figure 1.1. Habitat types at the Stability of Altered Forest Ecosystems (SAFE) project in Sabah Borneo. Sites represent a gradient of logging disturbance: most forest sites had been logged at least two times (labelled as logged forest), with additional logging rounds in the area that will be converted to plantation (experimental area). Primary forest is indicated by dark shading, bordering the experimental area as well as at Danum Valley conservation area (DVCA) and Maliau Basin conservation area (MBCA), located 36 km north and 69 km west of the SAFE project, respectively. The plantation mosaic is shown in orange, and blue lines indicate rivers. The black triangles represent locations for bat sampling, and the pink triangle is the oil palm location at which the mesocosms experiment was conducted.

CHAPTER 2

Spatial and temporal changes to insectivorous bat community diversity, abundance and composition

Hipposideros diadema, SAFE project

Abstract

Global biodiversity is in decline due to numerous local and global pressures, most notably habitat modification through logging practices. Understanding logging effects upon tropical forests is a major concern given that they harbour disproportionate levels of biodiversity and yet suffer the highest rates of conversion globally. .Here, I explored changes to insectivorous bat community diversity, abundance and composition across a broad, discrete gradient of degradation from primary to repeatedly-logged forest. Furthermore, I investigated interannual changes to community metrics, likely in response to short-term drought caused by El Niño. I predicted a strong response across the spatial gradient given the high intensity of logging events at the most degraded sites, and that amongst assessed community metrics composition would show the strongest response. I predicted generally weaker temporal changes due to potential lag effects from the time of environmental stress. Over the spatial logging gradient all community metrics except species richness were affected. Differences in community metrics among habitats were driven largely by differences between primary forest and other habitat types. Among-year differences were observed for all metrics except for community evenness, and similarly differences were strongly determined by altered values in subsequent years compared to 2011 'baseline' values. This work is important for informing management of tropical landscapes with regards to conservation value of habitats with different disturbance histories. From the metrics employed in this study, I conclude that all levels of disturbance altered communities by a similar degree from the structure and composition found in primary forests. These pronounced changes to bat assemblages detected over the spatial gradient are likely to have an effect on the wider community, cascading to lower trophic levels, and ultimately ecosystem functions retained within the ecosystem

Introduction

Global biodiversity is in sharp decline, and habitat loss and degradation combined are the most destructive threats (Hanski 2011; McRae *et al.* 2014). In tropical forests, habitat changes are caused primarily by demand for timber and commodity agricultural goods (Foley *et al.* 2005; Laurance *et al.* 2014; Gaveau *et al.* 2016). Degradation of tropical forests is of particular concern given the presence of disproportionately high levels of biodiversity (Bradshaw *et al.* 2009; Laurance *et al.* 2014) and their declines following land-use change (Gibson *et al.* 2011; Phalan *et al.* 2013). Large areas of agricultural land and logged forest are increasingly common features of tropical landscapes (FAO 2018). While biodiversity is lower in degraded forest than in primary forest at local, regional and global scales (Gibson *et al.* 2011), post-logging forests can support similar numbers of species to primary forests, across a wide range of taxa including mammals, birds, invertebrates and plants (Putz *et al.* 2012; Newbold *et al.* 2015). There is an urgent need to understand the conservation value of logged forest, and the importance of details such as management history, duration since logging and landscape context, *i.e.* proximity to suitable habitat (Malhi *et al.* 2014). Yet our understanding of the effects of logging on the ecology of tropical forest ecosystems remains limited due to the lack of baseline data in many studies (Laufer *et al.* 2013), incongruence in taxon-specific responses (Barlow *et al.* 2007; Thorn *et al.* 2018), and strong effects of spatial scale at which community studies are conducted (Berry *et al.* 2008).

Logged forests tend to have reduced structural complexity compared to their primary counterparts (Okuda *et al.* 2003; Asner *et al.* 2009; Rutten *et al.* 2015). Gaps in canopy cover following logging, *i.e.* from extracted and dying trees, expose the forest floor and alter environmental conditions such as temperature, humidity and soil moisture

(Hardwick *et al.* 2015). Field and remote-sensed measurements have also revealed more subtle changes in regenerating tropical forest, following selective logging: for example, canopy height and heterogeneity are reduced compared to primary forest (Okuda *et al.* 2003; Rutten *et al.* 2015). Vegetation structure is closely associated with habitat suitability for birds, mammals and insects (reviewed in Bergen *et al.* 2009), for examples, changes to leaf and twig density at multiple vertical levels can affect community assembly of tropical birds (Ansell *et al.* 2011) and mammals (Cusack *et al.* 2015). This agrees with theoretical explanations that increased structural complexity provides more niches (habitat heterogeneity hypothesis; Simpson 1949), and empirical observation of associated increased species diversity (Tews *et al.* 2004). Thus we would expect altered vegetation structure from logging to have observable impacts on habitat suitability and thus community metrics of various taxa.

The effects of logging on animal and plant richness can be minimal, with regenerating forests hosting 75 % of primary forest diversity (Putz *et al.* 2012), even following multiple logging cycles (Edwards *et al.* 2011). However, intensity of logging at the local and landscape scale have been shown to affect diversity response. For example, faunal species richness is negatively related to proximity to old-growth forest (Dent & Wright 2009), and to intensity of tree extraction, for vertebrate groups (Banks-Leite *et al.*, 2014). Where abundance has been quantified for tropical landscapes, patterns across land-use types, and among taxonomic groups are inconsistent (Gibson *et al.* 2011; Newbold *et al.* 2014). Species evenness is a major component of species diversity (Smith *et al.* 1996), describing how the relative abundances of different species compare. A community in which each species has similar abundance has high evenness, whereas a community in which species differ widely in abundance has low evenness. Generally, disturbed habitats are associataed with low evenness, as a few dominant species tend to thrive in altered environments (Mckinney *et al.* 2016). However evenness of tropical tree taxa has been found to be unaffected between logged and unlogged forest (Testolin *et al.* 2016). Despite, the incongruent responses of measures of diversity and abundance, the vast majority of studies have reported substantial shifts in community composition following logging, which can persist over multiple decades (Malhi *et al.* 2014), and potentially precede local extinctions (Meyer *et al.* 2015). Such changes can result from disparate effects of logging upon the demography of species, owing to specific life-history traits. Relative abundance shows strong guild-specific responses to logging for mammals (Wearn *et al.* 2017) and invertebrates (Cleary *et al.* 2005), and different responses even between closely related species of birds and mammals (Costantini *et al.* 2016).

Bats are considered to be particularly susceptible to human disturbance given their low reproductive rate, longevity and high metabolic rates (Voigt & Kingston 2015). For tropical bats, the majority of disturbance studies to date have been undertaken in the Neotropics, where forest assemblages are dominated by the family Phyllostomidae, and preferred mist netting techniques favour captures from this family (Castro & Michalski 2012). While there is evidence for expected declines in bat species richness in degraded forests (Medellín *et al.* 2000; Martins *et al.* 2017), and a higher sensitivity to reductions in native habitat than for other mammals (Muylaert *et al.* 2016), mixed responses among bat guilds are also documented (Presley *et al.* 2008). Far fewer studies have been conducted in the Old World forests, where bat assemblages are more difficult to sample due to the necessity for harp trapping. The response of those communities to environmental change, are likely distinct given that they are dominated by different major feeding guilds, insectivorous and frugivorous in the Paleo- and Neotropics, respectively. The majority of these species can be captured by harp-trapping in the forest understorey

(Kingston *et al.* 2003), providing very good indication of response for the entire assemblage. Depauperate assemblages in the Paleotropics are associated with degraded sites, and particularly with reduction in canopy closure and canopy height (Struebig *et al.* 2013).

I investigated changes in Old World assemblages of insectivorous bats across a gradient of logging disturbance in Sabah, Malaysian Borneo. South East Asia supports nearly 30% of the global bat fauna (Kingston 2010), and land use-change across the extent of species' range has led to concern over their conservation status. According to recent models, 21 bat species face a heightened extinction risk from the island of Borneo by 2080, when accounting for climate change and land-use change in combination (Struebig *et al.* 2015). I explored changes in diversity, abundance and community composition across a gradient of disturbance, from primary forest to repeatedly and intensively logged forest. Given the breadth of the spatial gradient of habitat quality, I expected decreases in total abundances and diversity metrics in heavily logged forest compared to primary forest habitat. More difficult to predict is the comparative response among disturbed forest with varying intensity and frequency of extraction. Assemblages comprise species with a range of ecomorphological traits, strongly associated with the suitability of different habitat type (Dodd *et al.* 2012; Blakey *et al.* 2017), and thus I expected of all community metrics, the most pronounced changes would be observed for community composition across the gradient of habitat degradation. Echolocation-associated differences in species' microhabitat and prey use likely contribute strongly to documented differences in assemblage composition in relation to affected landscape characteristics such as canopy closure and canopy height (Struebig *et al.* 2013; Bader *et al.* 2015; Martins *et al.* 2017), tree density (Hanspach *et al.* 2012), forest edges (Meyer *et al.* 2008) and connectivity (Frey-Ehrenbold *et al.* 2013). Furthermore, for bat assemblages sampled at the SAFE site I tested for among-year differences between a 'baseline' survey in 2011, and data from three consecutive years (2105 to 2017) during which there were emergent climatic stressors. Short-term responses are less likely to be reflected in the suite of metrics measured compared to changes associated with long-term structural changes to the habitat. However, given the severity of environmental perturbations experienced, *i.e.* intense El Niño-driven drought, I predicted decrease in total abundance during the height of the drought. The outcomes of this analysis provide whole community context for the taxonomically-constrained analyses of resource use and functional response conducted in subsequent chapters.

Methods

Bat sampling

I sampled bat assemblages at the Stability of Altered Forest Ecosystems (SAFE) project (Ewers *et al.* 2011), and primary forest sites Danum Valley Conservation Area (DVCA) and Maliau Basin conservation area (MBCA; refer to Tables 1.2 and 1.3 for logging history and active disturbance at all sites), although only adding the primary sites for the last two years. The SAFE landscape provided a gradient of logging disturbance: logged forest sites had been exposed to at least two rounds of extraction, with some experiencing additional logging rounds and further reduced forest cover. Logged forest site 'LFE' was only twice-logged and all logging ceased in the 1990s, allowing recovery in the intervening decades to tall forest with minimal canopy gaps. Indeed, of all the logged forest sites, 'LFE' is has vegetation structure most similar to primary sites. Sites 'E', 'C' and 'D' can generally be considered the most intensively disturbed with substantially lower measures of top-of-canopy height; leaf and twig density, particularly at strata above 30 m from the ground, and vegetation cover, when considering cover > 10 m from ground (measures are calculated from LiDAR-derived vegetation layers, and provided by T. Swinfield). Sites ‘F’ and ‘B’ were more limited in disturbance, with vegetation metrics intermediate of intensively disturbed sites and site ‘LFE’.

Sampling took place February – May 2015; March – July 2016, and May – July 2017. Sample sites within SAFE were located 2 to 7 km apart (Table 1.1). Thus, the distance between sites exceeded the mean home rage, 0.44 km^2 of insectivorous bat species (Struebig *et al.* 2013). Each year, I performed ten nights of trapping using six four-bank harp traps set along existing trails at each site (total 60 harp trap nights per site). Traps were checked at 20.30 and at 08.30, and moved each day by at least 20 m. For logistical reasons, site F was only sampled using 30 harp trap nights in 2015, and site ‘LFE’ was sampled three times in 2015, equating to 90 harp trap nights, due to low capture rates (see Fig. 2.1 for harp trap locations). On capture, each bat was identified to species where possible using external traits and basic dentation (Payne & Francis 2007). I also incorporated data from a landscape-scale sampling campaign of the SAFE project in 2011, offering community data prior to any active disturbance to the experimental area (see Struebig *et al.* 2013 for methods).

Statistical analyses

All statistical analyses were performed using the language environment R version 3.5.1 (R Development Core Team 2018). I compared community metrics among habitat types, assigning sites to the forest categories ‘primary’ (MBCA and DVCA), ‘twice-logged’ (LFE), ‘repeatedly logged intense’ (C, D and E) and ‘repeatedly logged moderate’ (B and F). To compare species richness, abundance and species evenness among forest habitats differing in disturbance history and among sampling years, I used generalise least square (GLS) models in R package *nlme* (Pinheiro *et al.* 2018). Site-specific species richness and abundance, both sensitive to sampling effort, were standardised by the number of harp trap nights employed per site. For species evenness, I selected Pielou's index of evenness, which is independent of species richness and therefore a complementary component to the latter in describing species diversity (Smith *et al.* 1996; Pielou 1997). I used the same modelling process to analyse the among-year differences for a subset of the data, including only SAFE sites, as among-year contrasts could be strongly influenced by the presence or absence of primary forest. In order to improve the assumptions of normality and homoscedasticity, I incorporated heterogeneity into the random component of the model by including the constant variance function, varIdent (Zuur *et al.* 2009), or reciprocal--transformed the response variables. For tests of among-year and habitat differences, Akaike information criterion (AIC) was used to optimise inclusion of site identity in the random component of the model. I undertook pairwise comparisons in R package *multcomp* to investigate among-year and among-habitat differences, and applied Bonferroni correction to account for multiple tests (Hothorn *et al.* 2008).

To explore bat community dissimilarity among habitats and years I analysed the four-year dataset of species-abundance in R package *vegan* (Oksanen *et al.* 2018). I applied Hellinger-transformation to raw abundance data in order to reduce the influence of outliers (Legendre & Gallagher 2001), and then applied PERMANOVA upon Bray-Curtis measures of dissimilarity between habitats and years. For tests among years, I accounted for the nested sampling design by constraining permutations to occur within sample sites. Although PERMANOVA is less sensitive to heterogeneity in dispersions than other permutation methods (Anderson & Walsh 2013), I first tested for homogeneity of dispersion among groups, *i.e.* habitats and years. In no instance was there rejection of homogeneity, and therefore rejection of the PERMANOVA null hypothesis can be interpreted more decisively as signifying different positions of communities in ordination space.

Results

Across three years of sampling I recorded 2913 bat captures. Of these, 2871 were annotated to species level, representing 43 different species, 15 genera and 4 families: Hipposideridae, Rhinolophidae, Vespertilionidae and Nycteridae. The Vespertilionidae were largely represented by the subfamilies Kerivoulinae and Murinae. Eight species, representing three of the four families, Hipposideridae, Rhinolophidae and Vespertilionidae (subfamily: Kerivoulinae), were particularly abundant, making up 90% of the dataset. Abundant species included *Hipposideros cervinus* and *H. dyacorum* within the Hipposideridae (leaf-nosed bats), *Rhinolophus sedulus*, *R. trifoliatus* and *R. borneensis* within the Rhinolophidae (horseshoe bats), and *Kervivoula intermedia, K. hardwickii* and *K. papillosa* within the subfamily Kerivoulinae (woolly bats). Across the landscape *H. cervinus* was the most consistently dominant species.

Species richness did not differ among habitats (GLS, $F_{3,20} = 0.199$, $P = 0.090$, Fig. 2.2A). However, species richness did differ among years (GLS, $F_{3,16} = 4.542$, $P = 0.017$, Fig. 2.2B). Post-hoc tests reveal that among-year differences are driven by reduced species richness in 2016 and 2017 compared to the 2011 baseline. Total abundance*, i.e.* number of individual bats, differed among habitats (GLS, $F_{7,20} = 13.76$, $P <0.001$, Fig.2.3A). Multiple comparisons reveal a clear pattern of increased abundance captured at primary forest sites, but no differences among logged forest with different disturbance histories. There were among-year differences in total abundance (GLS, $F_{3,16} = 7.519$, $P = 0.002$, Fig.2.3B) Post-hoc tests reveal that among-year differences are driven by reduced abundance in subsequent years compared to the 2011 baseline as well as a significant decrease in 2016 compared to 2015. Species evenness, measured by Pielou's index, differed among habitats (GLS, $F_{7,20}$ = 6.798, P =0.002, Fig.2.4A).Post-hoc between-site comparisons reveal this result to be driven by higher dominance in primary forest compared to all secondary forest classes. Species evenness did not differ among years (GLS, $F_{3,16}$ = 1.345, P = 0.295, Fig.2.4B). Community composition of insectivorous bats, based on Bray-Curtis dissimilarity, differed among both habitats (PERMANOVA, r^2 = 0.226, P = 0.003; Fig. 2.5A), and among years (PERMANOVA, r^2 = 0.224, P = 0.001; Fig. 2.5B).

Tables and Figures

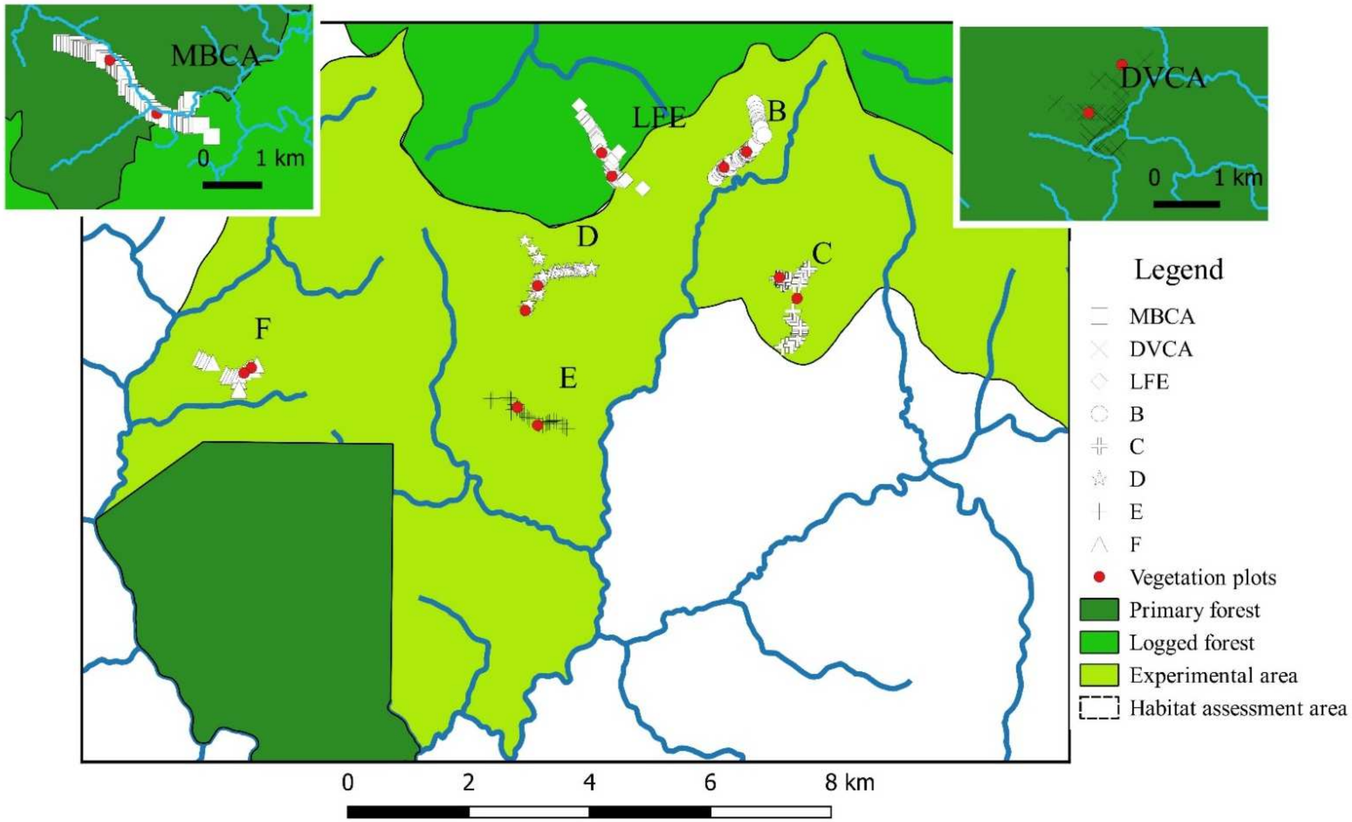


Figure 2.1. All harp trap locations used across the three years sampling, represented by site-specific symbols, and shown relative to vegetation plots (red dots).

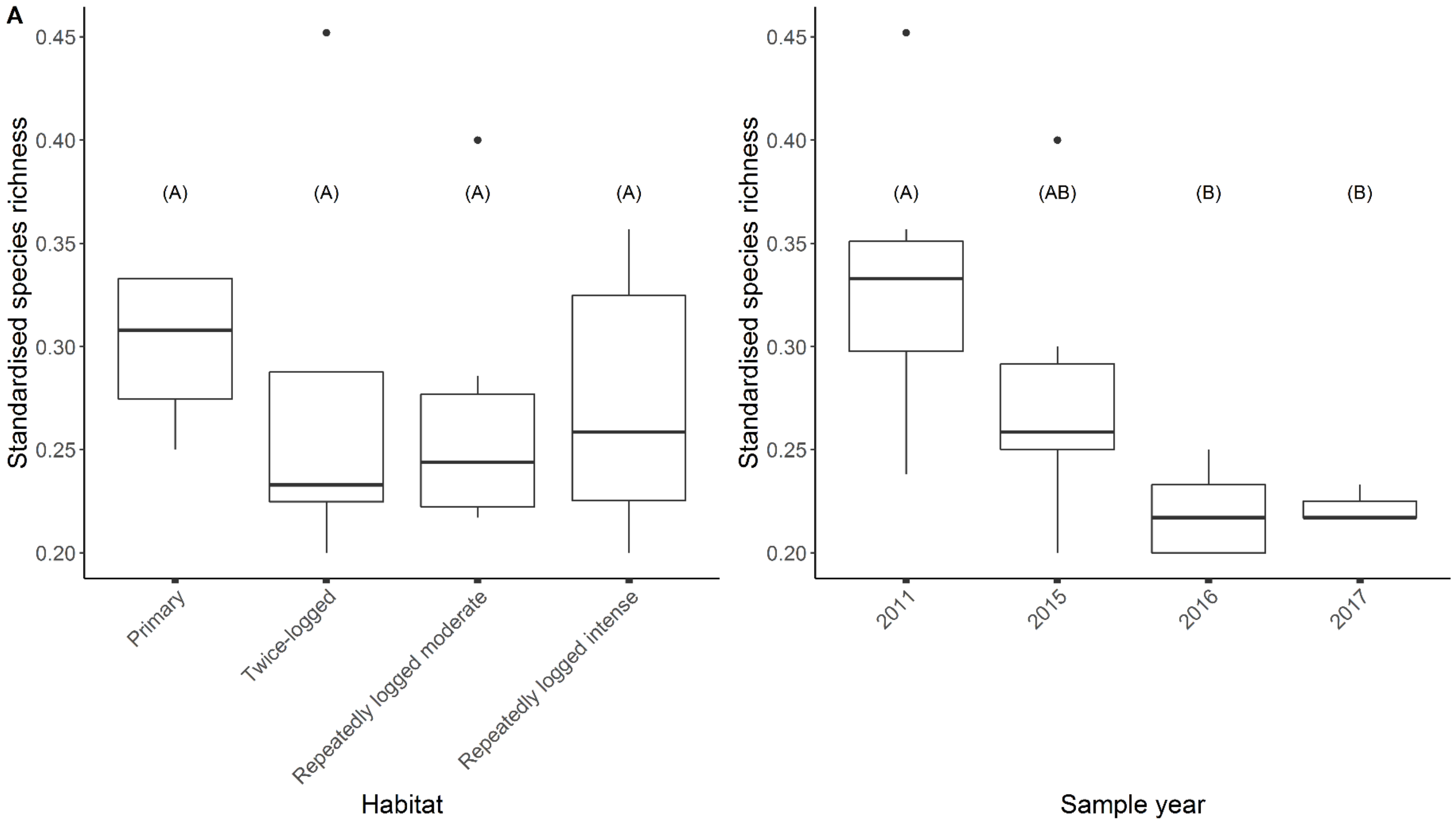


Figure 2.2. [A] Among-site and [B] among-year differences in species richness, the latter sub-setted to exclude primary forest sites. For both analyses total abundance was standardised by trapping effort, i.e. number of harp trap nights. Letters denote whether years were significantly different from one another (post hoc t-test, with Bonferroni correction for multiple tests).

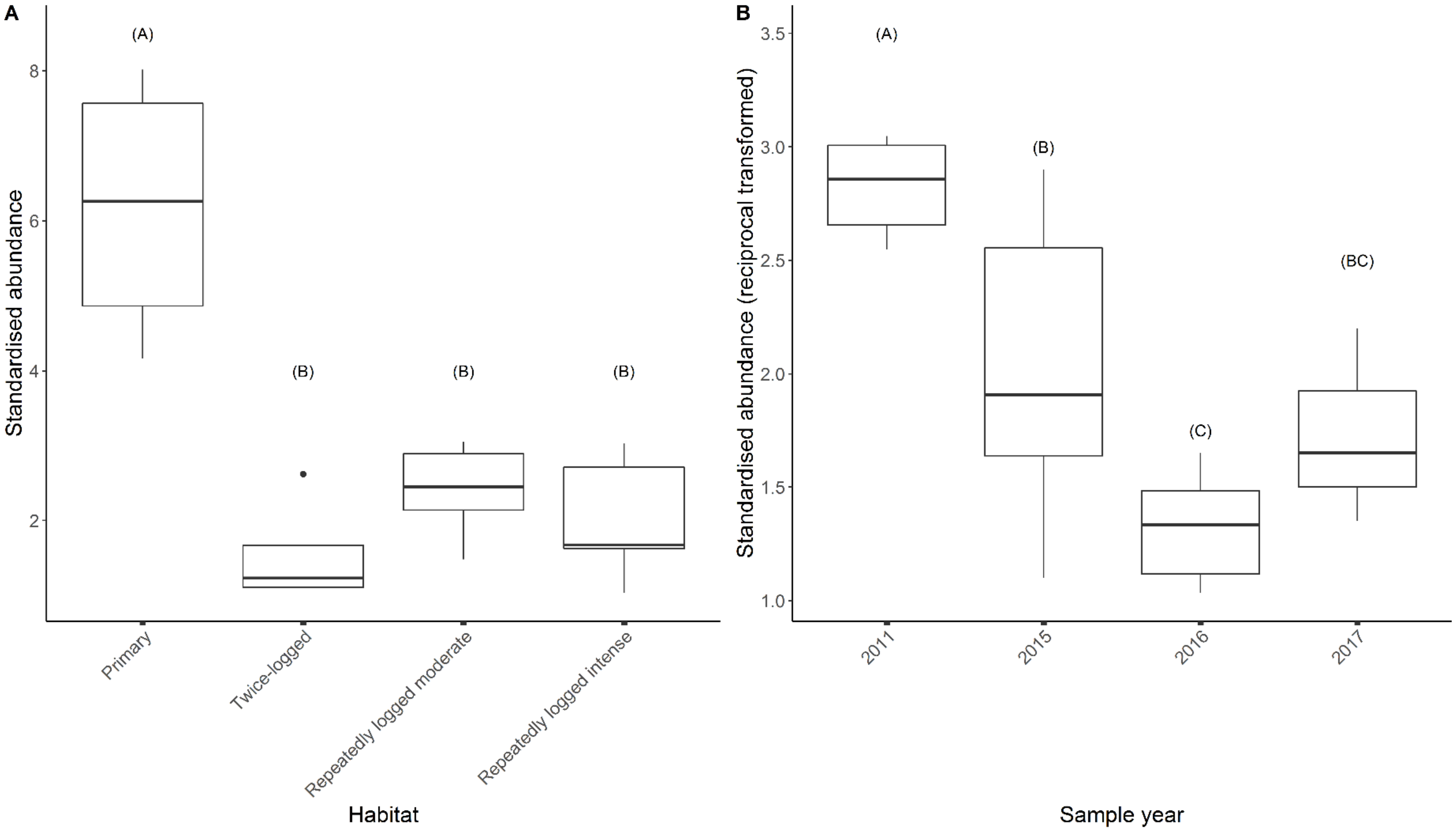


Figure 2.3. [A] Among-site differences in total abundance, and [B] among-year differences in reciprocal total abundance, the latter sub-setted to exclude primary forest sites. For both analyses total abundance was standardised by trapping effort, i.e. number of harp trap nights. Letters denote whether years were significantly different from one another (post hoc t-test, with Bonferroni correction for multiple tests).

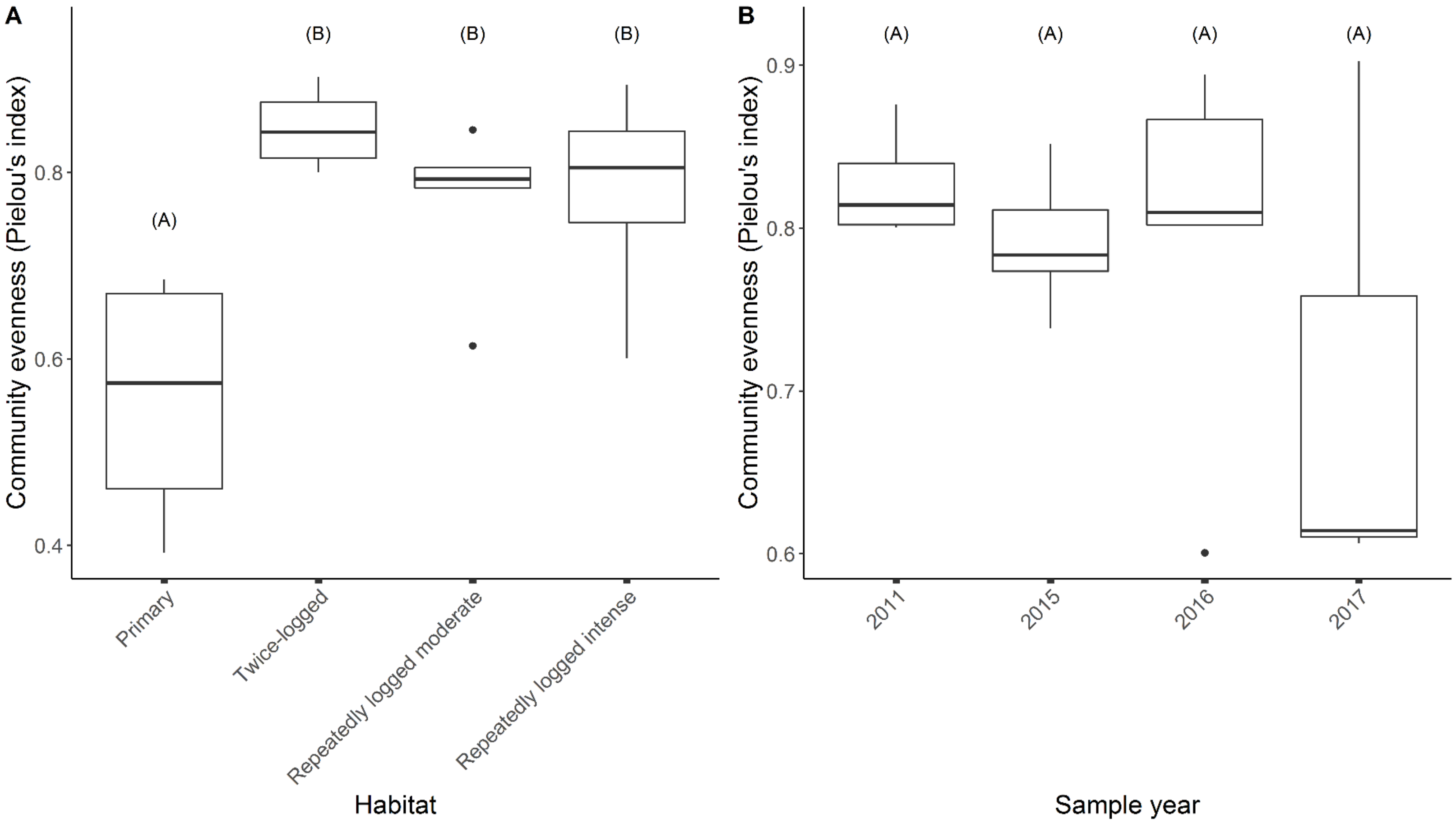


Figure 2.4. [A] Among-site differences, and [B] among-year differences in species evenness (Pielou's index), the latter sub-setted to exclude primary forest sites. Letters denote whether years were significantly different from one another (post hoc t-test, with Bonferroni correction for multiple tests).

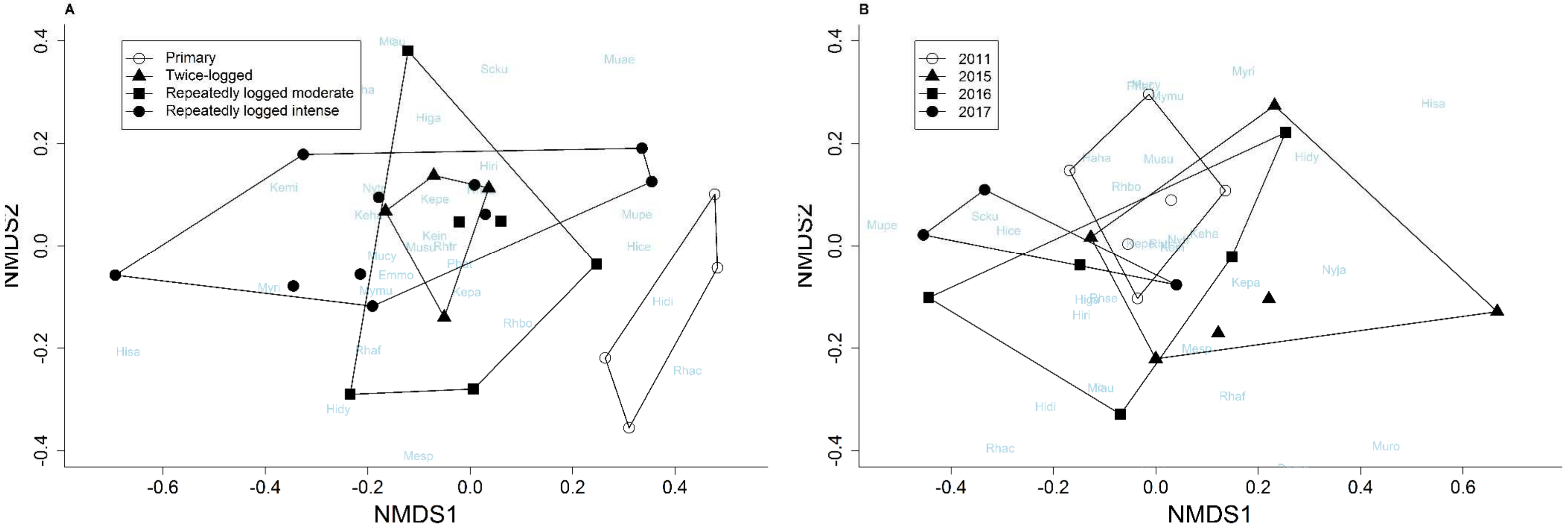
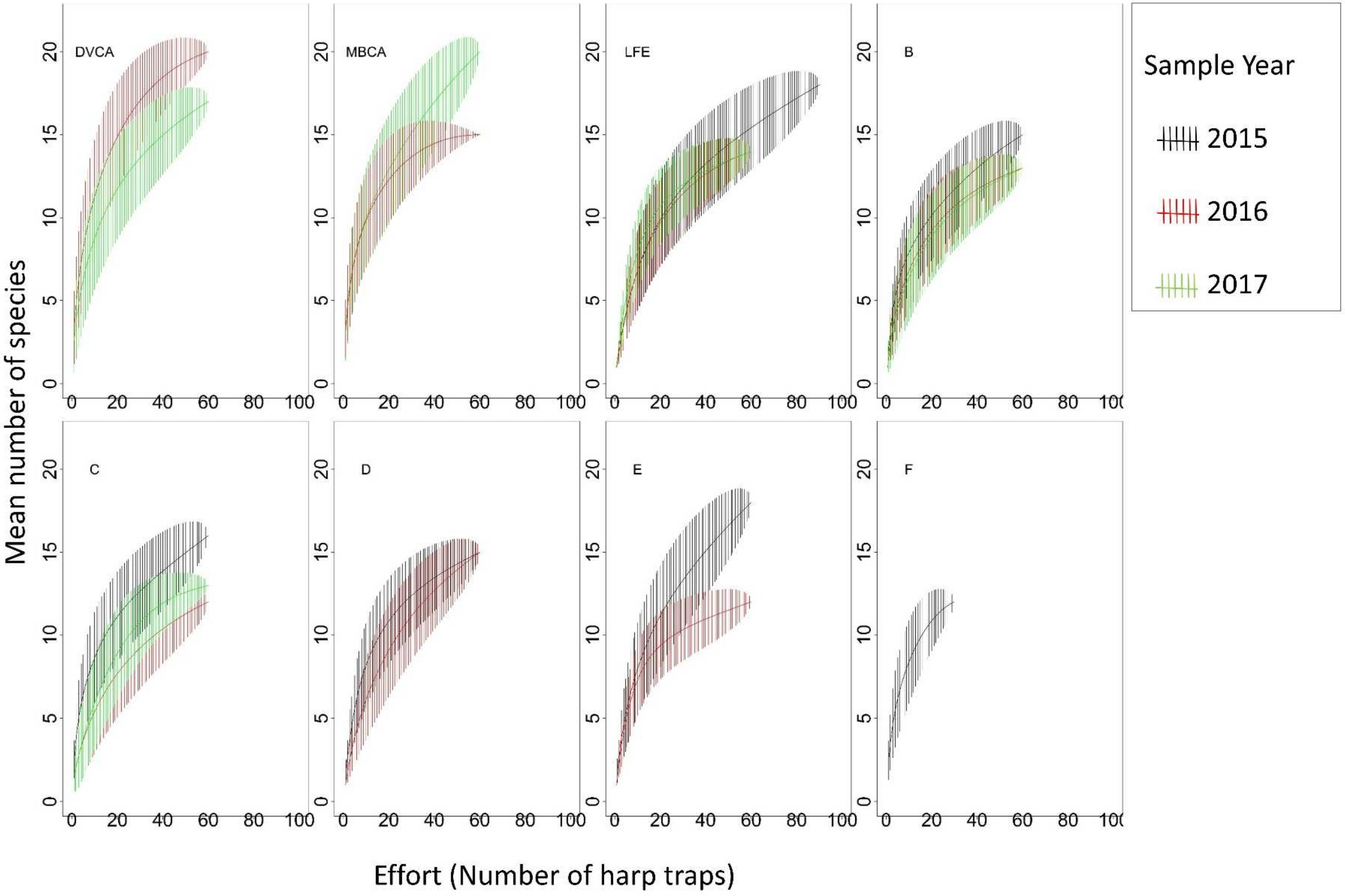


Figure 2.5. Non-metric multidimensional (NMDS) representation of community composition by [A] habitat type and [B] sample year. Mean community measures are shown as large symbols with contours drawn around community means from the same level of the grouping variable, i.e. [A] habitat type and [B] year [total number of communities = 24; unique combinations of site and year]. Communities are based on a matrix of raw species abundance [total species number = 41], and species are coded by four-letter binomial names in light blue. Stress = [A] 0.132 and [B] 0.09, linear fit [A] $R^2 = 0.226$; [B] $R^2 = 0.224$.

Figure 2.6. Species accumulation curves across all sampling sites, with sample years overlain. Each species accumulation curves is drawn for a community at a given site in a given year. The curved lines are accumulation curves, calculated by random method, *i.e.* harp traps are not added in the order they happen to be in the data. The vertical lines are the standard error around the mean species richness with each new trap addition. Where curves reach an asymptote it suggests that the trapping effort was substantial to survey the full assemblage species in the area, *i.e.* all species, which are able to be caught by harp trapping method.



Discussion

Overall, there were differences in bat species richness, total abundance, community evenness, and community composition, among habitat types representing a broad gradient of logging intensity as well as among sampling years. However, some metrics were unaffected over the spatial and temporal gradients: species richness was unaffacted by habitat, and community evennes was unaffacted by year. Differences in community metrics among habitats were driven largely by differences between primary forest and other habitat types. Similarly, among-year differences were strongly determined by altered values in subsequent years compared to 2011 'baseline' values. Although I did not look at interactions between local and global climatic pressures, the outcomes add weight to the need to consider multiple pressures in concert to protect the biodiversity of terrestrial tropical landscapes.

Species richness was lower in later years comapred ot the 2011 baseline values, i.e. prior to emergent stressors in the area (current human disturbance and climatic stress). The similarity between 2015 and 2011 is suggestive of a lag time between the point of disturbance and observable effects However, disturbed habitat of all quality levels did not show reduced richness compared to primary forest, in agreement with previous studies in the Neotropics (Clarke *et al.* 2005; Castro-Arellano *et al.* 2007). Generally, extirpation of predators at high trophic levels is one of the most pervasive consequences of habitat modification because of the high risk of local extinction associated with low population densities (Duffy 2003), large home ranges (Cardillo 2003), and unstable population dynamics (Davies *et al.* 2014). Due to habitat degradation and destruction, forest disturbance can negatively influence demographic traits such as fecundity and survival (Sodhi *et al.* 2009), which may lead to changes in concentration of local bat populations and local long-term extinction. The lack of changes in species richness among habitats could be due to replacement of locally extinct species. The obseved differences in among-habitat community composition adds some weght to this interpreation, although similarity is also highly influenced by relative abundance of a species within identical assemblages.Alternatively, among-habitat differences in topography and substrate could cause natural vairation in niche availability, and thusdiversity of species captured at disturbed sites could be bolstered by increased representation of suitable roosts for different species (Struebig *et al.* 2013). The most parsimonious explanation would be that it takes more time from the point of disturance for altered ecology to manifest in changed species composition. Given that we know very little regarding the resilience and resistance of local bat assemblages towards envionmental stressors, it is difficult to know whether sufficient time has elapsed. However, recent studies have shown very rapid responses in health of individual bats to disturbance (Seltmann *et al.* 2017).

On the other hand, long-term impacts on species richness among habitats may have been undetectable with our trapping effort. The absence of an aymptote in species accumulation curves (Fig. 2.6) for primary forest sites and twice-logged site 'LFE' indicates that the true species pool at these sites had not been captured with the applied sampling effort. By contrast, all repeatedly-logged SAFE sites plateaued after a sampling effort of approximately 15 harp traps, suggesting that the full species diversity in the area had been sampled. That LFE shows a similar trajectory to primary forest*, i.e.* no plateau, suggests this site is a good control within the SAFE experimental landscape, *i.e.* communities appear to be well recovered from previous disturbance. Undersampling, where present, was likely as a result of limited sample effort combined with low capture success, the latter for example owing to high number of capture days experiencing rainfall. Under representation can occur to varying degrees under different ecological conditions, and therefore introduces inaccuracy when comparing metrics among sites, or habitat types. In order to strengthen conculsions drawn from this study it would be appropriate to increase the sampling effort, whilst maintaing a standardised effort across sites. Indeed, a previous ecological inventory of insectivous bats in Borneo showed the capture of 300 individuals to be a sample effort which permits the majority of insectivorous bat species to be accounted for (Struebig *et al.* 2012).

There was a distinct reduction in total bat abundance in disturbed forest sites compared to primary forest sites. Given that assemblages were sampled over relatively uniform area, lower total bat abundance suggests reduced population densities. Reductions in total abundance can be driven by insufficient energy resources (Jara-Servín *et al.* 2017), for these assemblages, potentially manifesting in reduced recruitment in the preceding breeding season, or resettlement of wider ranging species to roosts in more high-resource locations. As discussed, this has not lead to long-term local extinction of species, as could be expected. For example, previous studies have shown concurrent changes in species richness and total abundance with habitat loss (Larsen *et al.* 2005). For out study, this may suggest that the carrying capacity in primary forest is very high, but that the population densities in lower quality forest do not fall below critical thresholds whereby demographic processes (*e.g.* recruitment, survival) are altered to such a degree as to prevent persistence of populations. Total abundance also differed among sample years, largely reflecting the among-year pattern in species richness However, abundance measures provide an indication of recovery following the peak of stress in 2016, given that 2017 abundance is comparable to the 2015 measure. Unfotunately the peak of current logging disturbance (2015) and impacts of El Niño (2016) are difficult to delineate in the analysis due to lack of quantification, and thus the conclusins regarding mechanisms of temporal changes are limited.

All disturbed forest was associated with increased species evenness, *i.e.* less variation in species representation, compared to primary forest, with the latter generally heavily dominated by the species *H. cervinus*. This was an unexpected result given that disturbed habitats are generally considered to be dominated by a few species. Dominance is thought to increase due to the relative success of very tolerant species in altered landscapes (Mckinney *et al.* 2016) owing to flexibility in resource use, for example (Edwards *et al.* 2013). Furthermore, species dominance can arise due to local invasion by species which would be controlled in healthy ecosystems (Brown & Gurevitch 2004). However, similar to my findings, logging in lowland forest of Amazonia was associated with decreased dominance of bat assemblages (Castro-Arellano *et al.* 2007). Our results, at least to some extent, reflect the capture of many *H. cervinus* from large roosts located in proximity to harp traps, *i.e.* roost availability and size is a factor in local dominance, interacting with other local biotic and abiotic characteristics (Struebig *et al.* 2013). Generally, there are relatively few studies investigating dominance, rather focusing on measures of richness and abundance. Where dominance is considered, the focus is on how patterns of local versus regional species dominance are impacted in post-logging forest (Summerville *et al.* 2009), and processes of spatial heterogeneity (Kitching *et al.* 2013). Changes in community evenness were not detected between years, suggesting that the proportional abundance of species remained relatively constant.

Community composition differed amongs habitats, in agreement with other studies documenting changes to proportional abundance of species in logged versus unlogged sites (Clarke *et al.* 2005; Peters *et al.* 2006). Changes to the proportional abundance of species indicates that species losses could become apparent in the longer term if forests are unable to recover (Meyer *et al.* 2015). Community composition also differed between years, by a similar magnitude to among-habitat changes (indicated by

R^2 values) These results are unsurprising given that compositional and structural differences to communities are commonly detected under human disturbance, and represent one of the clearer patterns from biodiversity studies of bat community responses (Meyer *et al.* 2015).

In the study of communities, different metrics have varying sensitivities to study approaches, such as sample effort or spatial scale of measurement. To overcome specific disadvantages of individual community metrics, previous studies have used indices to consider ecosystem health as a whole (Sodhi *et al.* 2009). Handling individual community metrics separately, I have been able to describe nuanced community changes among sites and years, which is useful for the interpretation of dietary changes observed in dominant bat species in subsequent chapters. Overall, I have documented pronounced changes to bat assemblages across the broad gradient of logging intensity from primary to repeatedly logged forest. From the community metrics assessed here, there is no indication that more moderately disturbed forest, or forest in later stage of recovery, is more similar to primary forest than intensively disturbed forest and thus not cannot be considered of any greater conservation value. However, observed structural changes to communities, *i.e.* altered relative species abundances, are known to alter ecosystem functioning (Ewers *et al.* 2015) and trophic interaction strengths (Barnes *et al.* 2014). Given that I did not account for life-history of the species making up the assemblages, I cannot investigate whether ther are more pervasive changes to the assemblages in terms of their ecological and functional intactness, as observed to be more sensitive than community changes in previous studues (De Coster *et al.* 2015).

Supplementary Tables

Table S2.1. Species-abundance for those abundant across the landscape, in addition to community composition metrics, ordered by ascending year for site-specific subgroups. Dominant species for each unique combination of sample site and year are highlighted in bold. *(n is total abundance; SR is number of species, and both metrics are standardised by number of trapping days)*

Site	Habitat	Year	*Hipposideros cervinus*	*H. dyacorum*	*Rhinolophus sedulus*	*R. borneensis*	*R. trifoliatus*	*Kerivoula hardwickii*	*K. intermedia*	*K. papillosa*	Pielou's evenness	n	SR
MBCA	Primary	2016	**124**	3	28	14	70	7	18	21	0.69	306	15
MBCA		2017	**104**	3	23	7	27	2	16	30	0.67	250	20
DVCA		2016	**311**	14	47	40	3	15	10	0	0.48	481	20
DVCA		2017	**328**	8	47	14	5	6	17	1	0.39	445	17
LFE	Twice-logged	2011	**19**	13	26	3	4	12	6	1	0.80	110	19
LFE		2015	7	11	26	15	4	7	**6**	4	0.82	99	18
LFE		2016	**14**	3	13	4	0	10	7	2	0.87	67	14
LFE		2017	**13**	8	12	6	6	7	5	12	0.90	81	14
B	Repeatedly logged moderate	2011	**31**	17	30	7	5	14	12	0	0.81	124	12
B		2015	20	25	27	2	1	7	**11**	0	0.78	127	15
B		2016	**23**	4	22	4	2	8	14	1	0.80	89	13
B		2017	**72**	3	24	0	4	5	10	4	0.61	132	13
F		2011	**36**	11	10	6	7	2	14	32	0.85	128	10
F		2015	9	9	25	2	4	0	**3**	21	0.78	81	12
C	Repeatedly logged intensive	2011	**37**	19	13	0	10	7	18	1	0.80	127	15
C		2015	**48**	36	34	0	6	7	17	1	0.74	174	16
C		2016	**58**	5	15	0	1	1	3	0	0.60	99	12
C		2017	**61**	3	9	0	3	4	3	0	0.61	99	13

D	2011	8	17	33	4	1	8	**14**	16	0.82	116	14
D	2015	0	15	20	1	1	0	**11**	15	0.85	97	15
D	2016	4	16	16	2	1	0	**3**	6	0.81	62	15
E	2011	8	22	21	0	7	**12**	8	6	0.88	107	14
E	2015	6	25	27	2	1	9	**9**	3	0.77	102	18
E	2016	8	10	14	3	1	14	**6**	11	0.89	80	12

Table S2.2. Model selection using Akaike information criterion (AIC) on bat population metrics to evaluate the fixed effects and their interactions. The best models are emboldened, *i.e.* those with the lowest AIC value (ΔAIC = 0) and distinguished from similar models with ΔAIC < 2 (Likelihood ratio test; P < 0.05), or the most parsimonious model when undistinguished.

Model number	Response	Fixed component	Random Component	AIC
1	**Species Richness**	**Habitat**	**NA**	**-32.470**
2	Species Richness	Habitat	varIdent(Site)	-26.356
1	**Species Richness**	**Year (subset)**	**NA**	**-30.228**
2	Species Richness	Year (subset)	Site	-28.228
1	**Abundance**	**Habitat**	**NA**	**30.790**
2	Abundance	Habitat	VarIdent(Site)	40.747
1	**Abundance (reciprocal)**	**Year (subset)**	**NA**	**0.593**
2	Abundance (reciprocal)	Year (subset)	Site	-1.043
1	**Peilou**	**Habitat**	**NA**	**-13.423**
1	Peilou	Habitat	varIdent(Site)	-7.147
1	Peilou	Year (subset)	NA	-16.270
2	Peilou	Year (subset)	Site	-17.658
3	Peilou	Year (subset)	Site, varIdent(Year)	-23.179
4	**Peilou**	**Year (subset)**	**varIdent(Year)**	**-24.008**

Table S2.3. Summary statistic for the best models (Tables S2.1.2), describing the response of bat community metrics among sample sites and sample years. Non-significant relationships ($P < 0.05$) are in grey.

Model	**Fixed component**	**Random component**	**F**	**Num DF**	**Den DF**	**P**
Species richness	Habitat	NA	0.199	3	20	0.090
	Year	NA	4.542	3	16	0.017
Abundance	Habitat	NA	13.76	3	20	<0.001
Abundance (reciprocal)	Year	NA	7.519	3	16	0.002
Community evenness (Peilou's index)	Habitat	NA	6.798	3	20	0.002
	Year	varIdent (Year)	1.345	3	16	0.295

F = F value, Num DF = numerator degrees of freedom, Den DF = denominator degrees of freedom, boldface indicates statistical significance with $P < 0.05$.

Table S2.4. PERMANOVA results based on Bray-Curtis dissimilarities of abundance data for insectivorous bat communities in relation to compartments a) sample site and b) sample year.

Grouping factor	Df	Sum sq	Pseudo-F	R^2	P-value
a) Site					
compartment	7	2.275	5.654	0.712	**0.001**
residuals	16	0.92		0.288	
total	23	3.195		1	
a) Year					
compartment	3	0.693	1.848	0.217	**0.001**
residuals	20	2.501		0.783	
total	23	3.195		1	

Df = degrees of freedom; Sum Sq = sum of squares; Pseudo-F = F value by permutation, boldface indicates statistical significance with $P < 0.05$, P-values based on 999 permutations (lowest P-value possible 0.001).

CHAPTER 3

Diet shift of mobile predator in response to narrow gradients of habitat quality and quantity

Bat trapping, site 'C' of the SAFE project

Abstract

Recent work indicates that degraded forests in late stage recovery can support species richness close to that of intact forests. In contrast, the impacts of forest degradation on trophic complexity and associated ecosystem functions remain poorly understood. Food web theory predicts that a predator's trophic position and niche breadth will decrease with habitat degradation, with negative consequences for community structure and ecosystem function. I applied stable isotope analyses to an important guild of high-level predators, insectivorous bats in tropical forest of Sabah, Borneo, and showed for the first time that across a landscape isotopic niche breadth contracts substantially (78%) over a narrow reduction (26%) in forest cover. I also demonstrate an increase in trophic position of high-level predators, indicating a lengthening of the food chain length with degradation. Importantly, I reveal functionally-important shifts in trophic pathways which discriminated among habitats more reliably than conventional community descriptors.

Introduction

Habitat loss and degradation together represent the leading threats to global biodiversity (Hanski 2011; McRae *et al.* 2014). In tropical forests, these changes are caused primarily by timber extraction and agricultural expansion (Foley *et al.* 2005; Laurance *et al.* 2014); around half of tropical forests now contain 50% or less forest cover (Asner *et al.* 2009). While biodiversity is lower in degraded forest than in primary tropical forest at local, regional and global scales (Gibson *et al.* 2011), recent studies indicate that the capacity of degraded forest to support primary forest species diversity increases with proximity to old-growth forest (Dent & Wright 2009), and percentage native cover

(Banks-Leite *et al.*, 2014), and that forests in the late-stages of recovery can support similar numbers of species to primary forests (Newbold *et al.* 2015).

Despite an urgent need to understand the conservation value of the remaining forest (Gardner *et al.* 2014), until recently the extent to which habitat degradation influences ecosystem functions had received little attention (Lewis 2009; Hector *et al.* 2011; De Coster *et al.* 2015). Recently, studies have begun to examine the effects of such modification on the functional and phylogenetic diversity dimension (Chapman *et al.* 2018). However, there remain calls for studies of anthropogenic impacts to move beyond assessments of species richness and to incorporate information on biotic interactions, and associated ecosystem functions (Antiqueira *et al.* 2017; Barnes *et al.* 2017).

Among the key ecosystem functions that may be modified by habitat degradation is the flux of energy and nutrients (Cardinale *et al.* 2012; Barnes *et al.* 2017). Such modifications may result from altered trophic structure, arising from changes to species interactions (Estes *et al.* 2011). High-level predators may respond to habitat change, and associated changes to prey composition, in a manner that fundamentally alters trophic structure and energy pathways throughout ecosystems (Tunney *et al.* 2014; Antiqueira *et al.* 2017), with far-reaching ramifications for healthy ecosystem functioning (Duffy 2003; Estes *et al.* 2011; Atwood *et al.* 2013). Such changes in trophic interactions that regulate the flow of energy and nutrients through ecosystems can be elucidated by tracing of predator's diets (Nielsen *et al.* 2018). In particular, the trophic position and niche breadth are important characteristics of predator diet, and can be strong indicators of community dynamics, stability and species persistence (Rooney *et al.* 2006; Kratina *et al.* 2012b).

The trophic position of an organism, representing the number of feeding linkages separating it from the producer level (Thompson *et al.* 2007), provides a quantitative measure of its trophic interactions. The trophic positions of high-level predators are strongly determined by food chain lengths, which for aquatic systems have been related to ecosystem size and resource availability (Post 2002a). In general, larger ecosystems and increased productivity support food webs with longer food chain lengths (Post 2002a), likely driven by increased trophic richness (Post & Takimoto 2007). I could therefore predict that habitat degradation is associated with a shortening of food chain length, and lower trophic position of high-level predators (Fig. 3.1). However, a recent meta-analysis highlights the interactive nature of these key environmental drivers upon food chain length (Takimoto & Post 2013), and theoretical work identifies omnivory (*i.e.* feeding at more than one trophic level) as an important determinant of the relationships (Ward & McCann 2017). For terrestrial ecosystems there is a lack of empirical data and theoretical work, making predictions difficult.

Stable isotope techniques provide a continuous measure of trophic position that allows capture of the complex interactions and trophic omnivory prevalent across ecosystems (Post 2002b; Thompson *et al.* 2007). Furthermore, isotopic bi-plots (*i.e.* $\delta^{13}C$ versus $\delta^{15}N$) offer a powerful method for characterising a species' (trophic) niche (Bearhop *et al.* 2004; Newsome *et al.* 2007), the most often studied component of Hutchinson's niche space. Bi-plots depict isotopic composition of food web elements in multivariate space (called "δ space"; Newsome et al. 2007). The subset of δ space occupied by the isotopic composition of an animal's tissues is the isotopic niche. The isotopic niche is not the ecological niche: Newsome et al. (2007) highlight the differences, and list the limitations of stable isotope in niche studies. However, the isotopic niche is a useful construct which can address questions traditionally limited by their dependence on describing the ecological niche. Natural variation in biological resources allows researchers to distinguish elements within food webs, and facilitates the exploration of trophic niches (Newsome et al. 2007). Quantitative analysis of stable isotope data offers a powerful method for capturing niche sensitivity to habitat degradation (Layman *et al.* 2007a; Jackson *et al.* 2011) and resource use (Newsome *et al.* 2007; Rader *et al.* 2016). To date, few studies have directly quantified the effect of environmental conditions on population niche breadth for high-level predators, possibly due to the difficulties of sampling sufficient numbers of individuals across multiple sites (Layman *et al.* 2007b; Dermond *et al.* 2017). Instead, most isotope studies draw comparisons between species at a single site (Dammhahn & Goodman 2013; Broders *et al.* 2014) or treat elemental isotopes separately (Edwards *et al.* 2013; Aliperti *et al.* 2017).

Here I apply isotope data analysis to estimate the trophic positions and niches of multiple high-level predator species across a landscape scale, and assess how these metrics are influenced by landscape- and local-scale forest degradation. I focus on forest-interior insectivorous bats, which are highly mobile, generalist predators and thereby represent an ideal model taxon for exploring the impacts of forest disturbance on community structure and energy fluxes through systems. Our focal species can be classified into two echolocation guilds based on their call types, which are linked to their feeding ecology (Schnitzler *et al.* 2003; Jacobs & Bastian 2016). Specifically, these bats comprise two high-duty-cycle (HDC) echolocators, specialised for detecting the fluttering wings of flying insects, and two low-duty-cycle (LDC) echolocators that use very broadband calls for detecting silent or even motionless prey, including spiders, located on or near to vegetation (Schmieder *et al.* 2012). These bats are highly sensitive to both habitat loss and quality (Kingston *et al.* 2003; Struebig *et al.* 2013). Similarly, their insect prey communities also negatively respond to tropical forest degradation, including reduced species richness, homogenisation of species composition, and shifts in trophic structure, driven by idiosyncratic responses of different taxa to altered biotic and abiotic conditions (Lawton *et al.* 1998; Barlow *et al.* 2007).

I hypothesise that the trophic position and niche breadth of high-level predators are influenced by both landscape- and local-scale logging impacts, and that changes to predator diet are stronger than changes to predator community composition due to the trophic flexibility prevalent in food webs (Tylianakis *et al.* 2007). Specifically, I predicted that increased forest degradation would strongly reduce isotopic niche breadth, and lower trophic position, of focal bat species (Fig. 3.1). I also expected that echolocation guilds would differ in isotopic niche and mean trophic position, and that LDC echolocators that feed on a wide range of insect groups would correspondingly show stronger negative proportional response of both dietary metrics to habitat degradation.

Methods

Study sites and habitat characterisation

To sample bats for isotope analyses, I conducted fieldwork between February and June 2015 at the Stability of Altered Forest Ecosystems (SAFE) Project. I focused on bats at six forest sites all of which have been subjected to selective logging, but of varying number and intensity (Ewers *et al.* 2011; See Fig. 2.1 main map for site locations in the SAFE landscape) resulting in a range of forest cover at the 3 km extent from 16 – 96%. Spatial heterogeneity in forest degradation is due to differences in proximity to areas of remnant intact forest (landscape-scale) and selective removal of the most valuable timber, and features such as logging roads (local-scale). At each site I obtained vegetation samples from two 25 m^2 permanent plots located at least 400 m apart (mean 446m, SD 14m) with the exception of one site where, for logistical constraints, the plots were only 150m apart. All 12 study plots form part of a wider network of plots across the SAFE landscape, and also vary in levels of local disturbance due to localised differences in timber extraction and proximity to logging roads (Ewers et al., 2011).

I characterized levels of forest degradation at each plot using a range of metrics. To consider the quality of the wider habitat in which plots are embedded I estimated forest cover for 1 km and 1.5 km radii of each plot centre using data in Hansen *et al.*, (2013). To capture local habitat quality I calculated carbon density (as a measure of above-ground biomass) within a 50m buffer of the plot centre; canopy height as a point measure at the plot centre using high resolution (100 m^2 and 2 m respectively) LiDAR datasets collected in November 2014 (Coomes *et al.* 2017); and percentage cover of trees and grass in each 25m^2 plot from the SAFE core data repository. In a few cases, where either the plot centre fell outside of the LiDAR coverage, or where SAFE core data were unavailable, I recorded the data as missing (for sample sizes see Table S3.1).

Bat sampling

I undertook two rounds of bat trapping across the study area, visiting the six focal sites sequentially such that sites visits were at least a month apart. Sites were visited in a random sequence, i.e. independent of the level of disturbance and minimising any confounding temporal effects. At each site during each sampling round, I performed five nights of trapping using six four-bank harp traps set along existing trails (1-1.5 km) around the two plots (total 30 harp trap nights per site). Traps were checked at 20.30 and at 08.30, and moved each day by at least 20m. In total, four sites were visited twice (60 trap nights), one was visited once (30 trap nights) for logistical reasons, and the least disturbed site ('LFE') was sampled three times to obtain control data (90 trap nights). The mean distance of any bat trapping location from the nearest plot is 600 m (SD 624 m).

On capture, each bat was identified to species and, for adult individuals, a wing membrane biopsy was taken using a 3 mm punch (Schuco, Walford, UK) for stable isotope analyses and placed in separate tubes for same day processing. Heavily pregnant or recently recaptured bats were not sampled. All individuals were released at the point of capture. For each trap, to account for the effect of aquatic prey inputs into bat diets, I calculated distance to the nearest stream using the R package *rgeos* (Bivand & Rundel 2016). Freshwater food web elements can have a distinct C-N stable isotope composition from terrestrial elements (Milligan *et al.* 2010), and therefore when aquatic inputs are putative prey for bat species, we may detect a signal in isotopic parameters along a gradient of stream proximity. In this study we used proximity to stream to delineate this response from that resulting from logging effects. Streams were identified by D Orme based on images obtained by the Shuttle Radar Topography Mission (https://www.safeproject.net/dokuwiki/safe_gis/stream_networks).

To characterise predators' population-level diet use across a gradient of habitat disturbance, I focused on four dominant bat species that together accounted for 63% of all captures. These species comprise two HDC echolocators: *Hipposideros cervinus* (family Hipposideridae), *Rhinolophus trifoliatus* (family Rhinolophidae), and two LDC echolocators: *Kerivoula intermedia* and *K. hardwickii* (Vespertilionidae, subfamily Kerivoulinae). Bat species from these genera are among the most abundant members of forest-interior bat assemblages in the Old World tropics (Struebig *et al.* 2012) and typically specialise in foraging for insects either on or near to dense vegetation ('narrow-space').

Stable isotope analyses, trophic position and niche breadth

I performed stable carbon and nitrogen isotope analyses of bat tissue samples as well as plant basal resources. The latter provided an essential baseline for accurate calculation of predators trophic position (Post 2002b), which accounted for both temporal and spatial changes in ^{15}N associated with local nitrogen inputs, caused by habitat degradation, *e.g.* logging or seasonal changes (Ponsard & Arditi 2000; Popa-Lisseanu *et al.* 2015). Local ^{15}N baselines were strictly time-matched to predator isotope samples, which accounts for enriching effects of aridity upon $\delta^{15}N$ of terrestrial predators sampled during relatively dry months (Popa-Lisseanu *et al.* 2015). Since leaf $\delta^{13}C$ displays a substantial vertical gradient, decreasing towards the forest floor, due to the canopy effect upon carbon isotope discrimination and changes in the $\delta^{13}C$ of source air (Buchmann *et al.* 1997), baseline plant matter was collected from a narrow strata, i.e. 0 – 2 m from the ground. To provide maximum resolution, and to increase the ecological relevance of environmental metrics for a bat community with relatively narrow home range (for these species, approximately 0.44 km^2; Struebig *et al.* 2013), I calculated predator dietary metrics at the sub-site level (two plots per site). I allocated bat individuals to populations based on the proximity of their capture sites to the 12 focal vegetation plots (see Table S3.2 for sample sizes). I collected primary producers (C_3 understory plants) from each of the 12 vegetation plots, providing plot-specific ^{15}N isotopic baselines (Table S3.3). The mean distance of bat trapping locations from the nearest vegetation plot was 306m (SD 280m).

I dried vegetation samples at 60°C for a minimum of 48 hours (Hyodo *et al.* 2010) and wing membrane samples (< 0.3 g wet mass) at 60°C for 2hrs. Vegetation samples were ground to a fine powder using a ball mill (Retsch UK Ltd., Hope, UK). I then weighed all samples into 6 x 4 mm ultraclean tin capsules (Elemental Microanalysis Ltd., Okehampton, UK) using an ultra-microbalance (± 1µg; Mettler-Toledo, Greifensee, Switzerland) to provide sufficient elemental carbon and nitrogen for analysis by continuous flow isotope ratio mass spectrometry (SERCON, Crewe, UK; for weights see Supplementary methodology 3.1). Due to their low mass (total N content of ~ 7µg) bat tissue samples were analysed in low volume reaction tubes within the elemental analyser to maximise solid to gas conversion efficiency, and I amended operating settings accordingly (for details see Supplementary methodology 3.2).

Isotope ratios are expressed in per mil (‰) relative to international reference standards ($R_{standard}$), which are Atmospheric Nitrogen and Vienna PeeDee Belemnite (VPDB) for nitrogen and carbon, respectively. To correct predator isotope values for a blank effect, I used a mass balance weighted mean equation to solve for the $\delta^{15}N$ value of the blank (Fry & Brand 1992), inputting data from a nitrogen dose series spanning beyond the breadth of nitrogen content in predator tissue (5 to 73μg). See supplementary methodology 3.3 for quality control of delta values on wing tissue samples.

To calculate the mean trophic position for the four dominant predator species per plot, I used the equation:

$$\text{Trophic Position} = 1 + (\text{bat wing } \delta^{15}N - C_3 \text{ plant } \delta^{15}N) / 3.4, \qquad \text{(eq. 1)}$$

where 1 represents the trophic position of C_3 plants, and 3.4 the $\delta^{15}N$ enrichment per trophic level (Post 2002b).

I also characterised the isotopic niche breadths of the four dominant bat species per plot, by calculating the modal Bayesian ellipse area, SEA_b in the package *SIBER* (Jackson *et al.* 2011). This approach accounts for uncertainty in predator isotopic values and is inherently insensitive to sample size. I only included samples with at least five conspecific bat individuals from the same plot (Jackson *et al.* 2011).

Statistical analyses

For initial overview of the isotopic data from wing tissue of focal species, the effect of species identity upon trophic position was analysed using two-way ANOVA. Furthermore, to introduce the ^{15}N-isoscape of the forest sites, the effect of site identity upon leaf $\delta^{15}N$ was analysed using two-way ANOVA. Thereafter, I used generalised least squares (GLS) models in R package *nlme* (Pinheiro *et al.* 2018) to determine the impact of habitat degradation on SEA_b and trophic position of bat predator populations, while accounting for species identity as a random factor. LME models with random intercept allowed species to vary, but with a common slope for the fixed environmental variables (Zuur & Ieno 2016). Although I only had four dominant species (levels of the random factor), the benefits of handling the variance hierarchically are known to outweigh costs of shrinkage (Harrison *et al.* 2018). SEA_b and mean trophic position data were log-transformed to meet the assumptions of normality and homoscedasticity of the residuals. In order to detect spatial autocorrelation in the data I tested correlation between geographic distances and distances between measured outcomes using *vegan* (Oksanen *et al.* 2018). There was no correlation between inter-site geographic distance and inter-site differences in trophic position (Mantel $r = -0.182$, $P = 0.871$) or niche breadth (Mantel $r = -0.237$, $P = 0.916$), suggesting that that ecological distances between sites were not strongly associated with geographic distances between sites, and I therefore considered plots to be independent for the purposes of analysis. Although I did not detect spatial structure in the distribution of the response variables, I also tested models with different spatial autocorrelation functions incorporated into the random component of the models (Pinheiro & Bates 2000; Petermann *et al.* 2015). Spatial autocorrelation did not have any effects, and thus I present models without autocorrelation structure (for details see Supplementary methodology 3.3). In the maximal model I included those explanatory variables which had estimates available for all plots, and which were not strongly intercorrelated (see Fig. S3.3 for collinearity analysis of explanatory variables), in order to maximise statistical power and prevent collinearity in the analyses. The maximal models included forest cover (1 km extent), canopy height and proximity to stream. From the maximal fixed structure, containing all explanatory variables, I used model simplification with the drop1 function to remove variables which did not significantly improve the model. No interactions between terms were included in order to avoid overfitting given a small number of populations (n < 30, supplementary Table S3.5). Although this constraint prevented us from defining the best predictive model, it allowed us to reveal significant relationships between dietary metrics and individual predictors. For the final model, I used restricted maximum likelihood (REML) estimation of model parameters, which is a preferred method for smaller samples.

I used linear models in the core package *stats* to determine the impact of habitat degradation on predator community structure, including data from all bat captures annotated to species level. I tested for among-site differences in species richness, Shannon-Weiner diversity index, and Pielou's index of community evenness. Maximal models included the same set of environmental variables in order to directly compare the strength of dietary and taxonomic responses. As above, model simplification was conducted using the drop1 function. Furthermore, I used multivariate analyses upon a trap-level species-abundance matrix to test for among-plot differences in community composition. I applied PERMANOVA upon Bray-Curtis measures of dissimilarity between plots, with trap identity as a nested factor.

I applied GLS models to identify whether echolocation guild (fixed factor) is a good predictor of SEA_b and trophic position, while accounting for plot identity as a random factor. I also tested for differences in isotopic means between echolocation guilds using an unpaired t-test. Furthermore, to compare the dietary responses of echolocation guilds, I employed ANCOVA in *lme4* to test the effect of habitat degradation on SEA_b and mean trophic position, whilst including echolocation guild as a covariate. Where interactions were significant ($P < 0.05$), I compared models using ANOVA F statistics to assess whether the interactions significantly improved model fit. All analyses were performed in R 3.5.1 (R Development Core Team 2018).

Results

Across the 12 plots I recorded species-level information for 536 insectivorous bats representing 26 species. I analysed 340 wing punches from a subset of the four dominant species to characterise population-level dietary information. In total. 134 captures were made for *Kerivoula intermedia* across the six sample sites, 96 for *K. hardwickii,* 66 for *Hipposideros cervinus* and 44 for *Rhinolophus trifoliatus.* In terms of populations of sufficient individuals to derive trophic metrics, *Kerivoula intermedia* was best represented across the gradient with 10 viable populations, and *Hipposideros cervinus* and *Rhinolophus trifoliatus* were the least well represented, each with only 4 viable populations. Across the entire dataset, the four focal species have significantly different trophic positions (ANOVA, $F_{3, 339} = 15.44$, $P = <0.001$), and Tukey post-hoc tests indicate that the only species which are not different are the two species of Kerivoulinae. *K. hardwickii* had the highest trophic position 3.818 (SD 0.402) and *R. trifoliatus* the lowest position 3.177 (SD 0.390). The wing tissue from the four species was also found to have significantly different $\delta^{13}C$ values (ANOVA, $F_{3, 339} = 41.93$, $P = <0.001$), and Tukey post-hoc tests indicate that it is only comparisons between species of the same echolocation guild which are non-significant (*K. intermedia: K. hardwickii* and *H. cervinus; R. trifoliatus*). The $\delta^{15}N$ signatures of plants representing the baseline of the food web was significantly different between sites (ANOVA, $F_{13, 155} = 2.778$, $P = 0.001$). At the extremes values varied from -2.04 (SD 1.23) ‰ at the least disturbed site 'LFE' to 2.09 (SD 1.68) ‰ at heavily logged site 'E'.

Isotopic niche breadth showed a 78% reduction with ~26% proportional decline in forest cover at the 1 km scale (GLS, $F_{1,21} = 7.178$, $P = 0.014$, based on the slope of the line in Fig. 3.2A, $n = 26$). There was a significant reduction in mean trophic position with decrease in canopy height (GLS, $F_{1,21} = 13.667$, $P = 0.001$, Fig. 3.2B, $n = 26$). No other environmental characteristics were retained in the optimal models, *i.e.* did not significantly alter isotopic niche breadth or trophic position of bat predators.

None of the environmental variables were retained in the best models explaining differences in Shannon-Weiner index or Pielou's index. Proximity to stream was retained in the best model describing among-plot differences in species richness, but the effect was non-significant (LM, $F_{1,10} = 3.008$, $P = 0.114$). Community composition did not differ between vegetation plots (PERMANOVA, $R^2 = 0.012$, $P = 1$; supplementary Fig. S3.4).

The two echolocation guilds consistently differ in the location of their isotopic niche in bi-plots (Fig. 3.5), and in both mean $\delta^{15}N$ and mean $\delta^{13}C$, across all six sampling sites ($P < 0.0001$). Tissues of LDC echolocators were significantly ^{13}C-enriched (-23.988 ± 0.078 ‰, mean ± 95 % CI, n = 340) compared to HDC echolocators (-24.548 ± 0.058 ‰, n = 340). Populations of LDC echolocators were significantly ^{15}N-depleted (7.919 ± 0.169, n = 340) compared to HDC echolocators (8.505 ± 0.119, n = 340). Furthermore, after accounting for differences among forest plots, I detected significant differences between the two echolocation guilds in their isotopic niche breadths (GLS, $F_{1,21} = 9.643$, $P = 0.005$) and mean trophic position (GLS, $F_{1,15} = 26.035$, $P < 0.0001$).

In terms of guild-specific response to environmental characteristics, HDC echolocators responded more strongly to local habitat quality than LDC echolocators (LM, tree cover x guild, $F_{3,13} = 6.981$, $P < 0.001$, Fig. 3.4A; grass cover x guild, $F_{3,13} = 6.981$, $P < 0.001$, Fig. 3.4B). Across the suite of habitat characteristics, there was no other interactive effect of echolocation guild which would improve the model fit for isotopic niche or trophic position (supplementary Tables S.5 & 3.6).

Tables and Figures

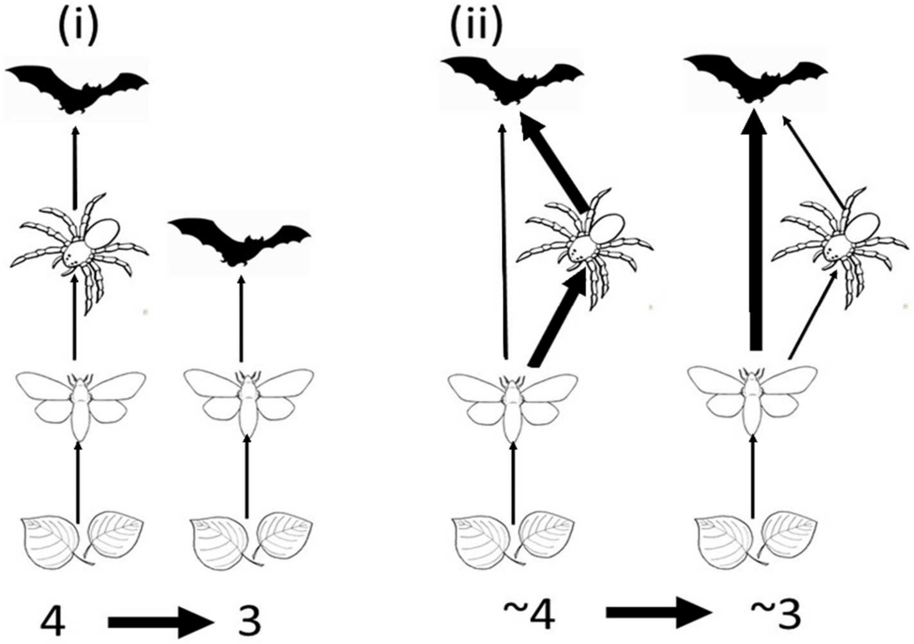


Figure 3.1. A conceptual diagram representing the mechanisms that could lead to changes to trophic position of the predator (adapted from Post & Takimoto 2007), where the arrows between organisms represent the magnitude of vertical energy flow. I tested the effect of habitat modification on the length of food chain composed of resources (plants), intermediate consumers (insects) and high-level predators (bats). Under habitat degradation the trophic position of high-level predators would be expected to decrease following (i) the removal of intermediate predators, *e.g.* spiders, and (ii) an increase in the degree of trophic omnivory, *i.e.* greater dietary contribution from trophic positions other than that directly below. If the habitat degradation alters arthropod guild composition, for example shifting to dominance by herbivores, I would also expect an associated decrease in the population niche breadth of bat predators.

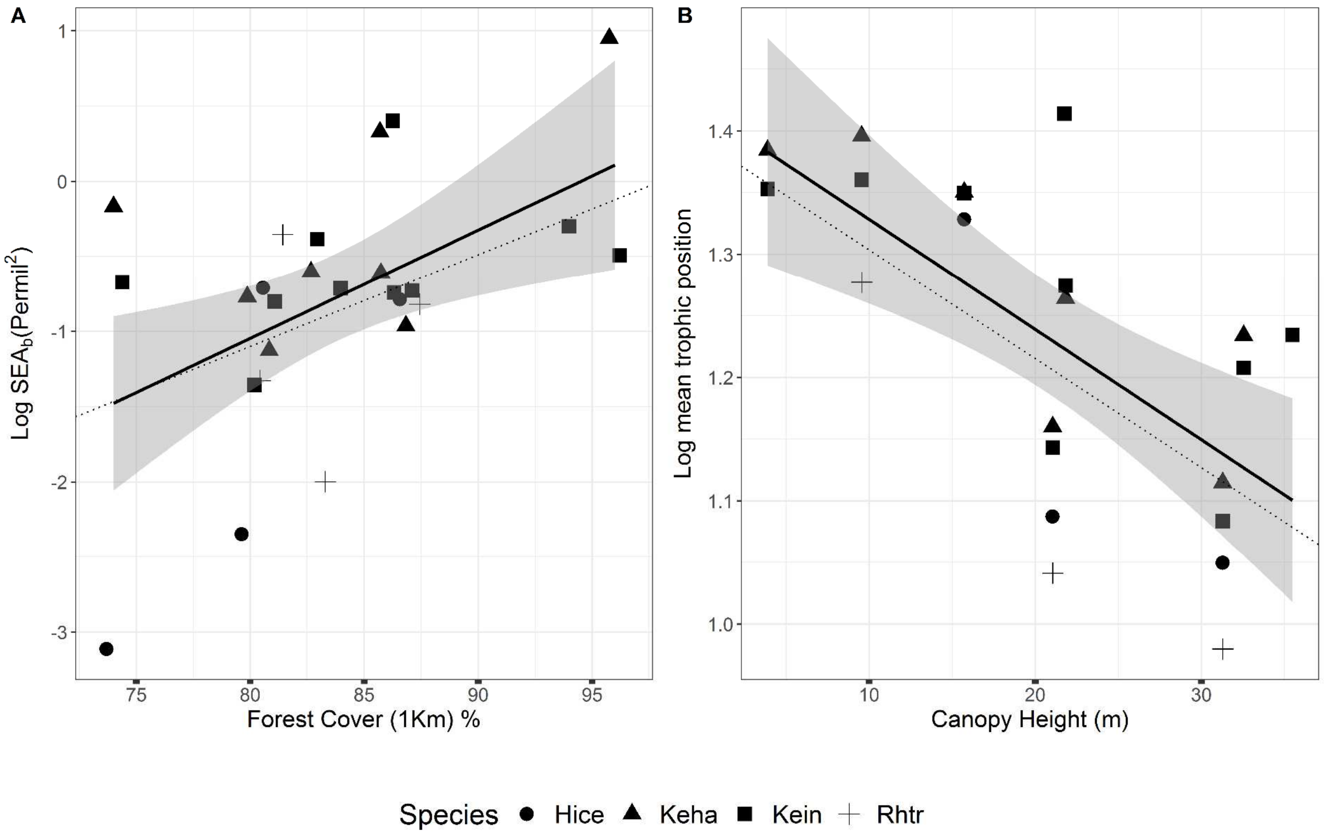


Figure 3.2. Responses of bat populations' [A] isotopic niche breadth to forest cover at the 1 km scale (LME, $F_{1,21}$ = 7.178, $P = 0.014$) and [B] trophic position to the changes in canopy height (LME, $F_{1,21}$ = 13.667, $P = 0.001$). The populations include five or more conspecific individuals captured at harp trap locations within a sampled vegetation plot. Bold lines depict the fitted linear model and dotted lines represent slope and intercept coefficients from the LME model. The slope coefficients ± 1 SE, estimated from the LME models are [A] and [B] -0.009 ± 0.002.

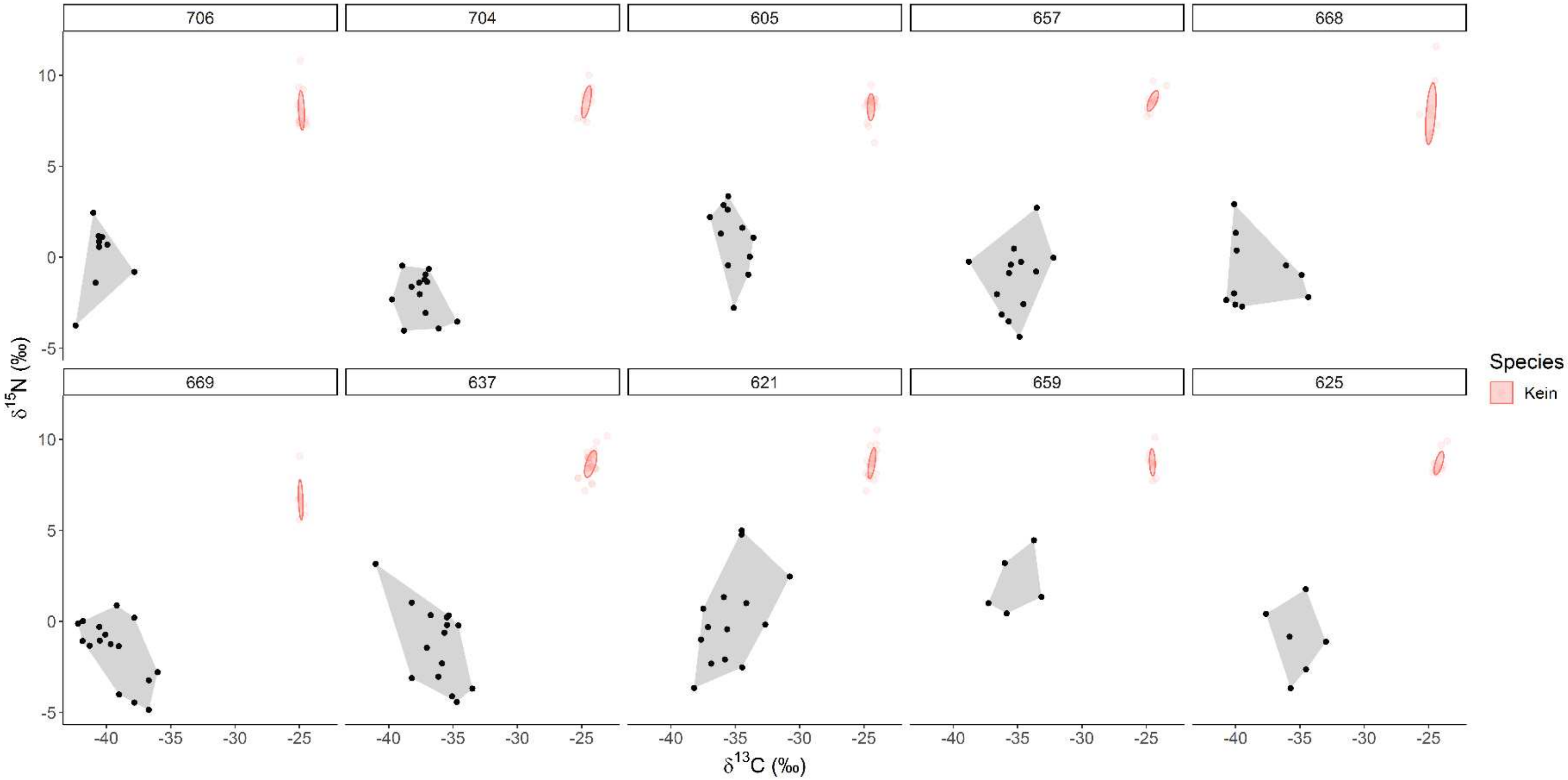


Figure 3.3. Site-specific isotopic niche breadth of the most common focal species, *Kerivoula intermedia,* plotted alongside the site-specific variation in stable isotope compositon of leaves at the base of the food chain. The isotopic data from wing tissue of individual bats is plotted as light red circles and isotopic niches, representing 40 % of population variance, are plotted as dark red ellipses. Each black point is a leaf sample, and convex hulls are plotted around the most extreme leaf samples in terms of their bivariate isotopic composition. Sites are ordered by decreasing % forest cover (1 km extent); top left to bottom to right.

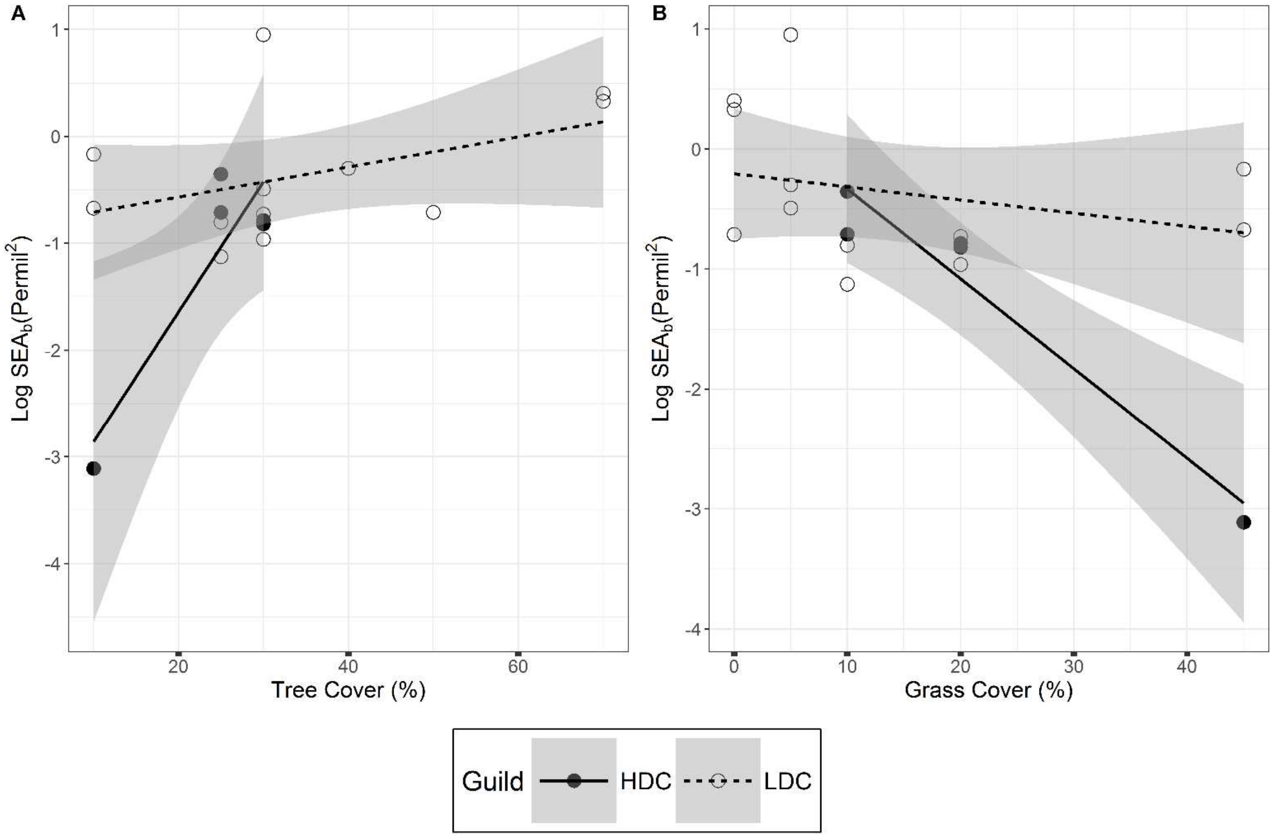


Figure 3.4. The responses in isotopic niches to the changes in [A] percent tree cover and [B] percent grass cover between the two echolocation guilds (LM, tree cover x guild, $F_{3,13} = 6.981$, $P < 0.001$) and (LM, grass cover x guild, $F_{3,13} = 6.981$, $P < 0.001$) respectively. High-duty-cycle (HDC) echolocators are represented by circles and solid line, whereas low-duty-cycle (LDC) echolocators are represented by triangles and dashed line. Populations include five or more conspecific individuals captured at harp trap locations within a sampled vegetation plot.

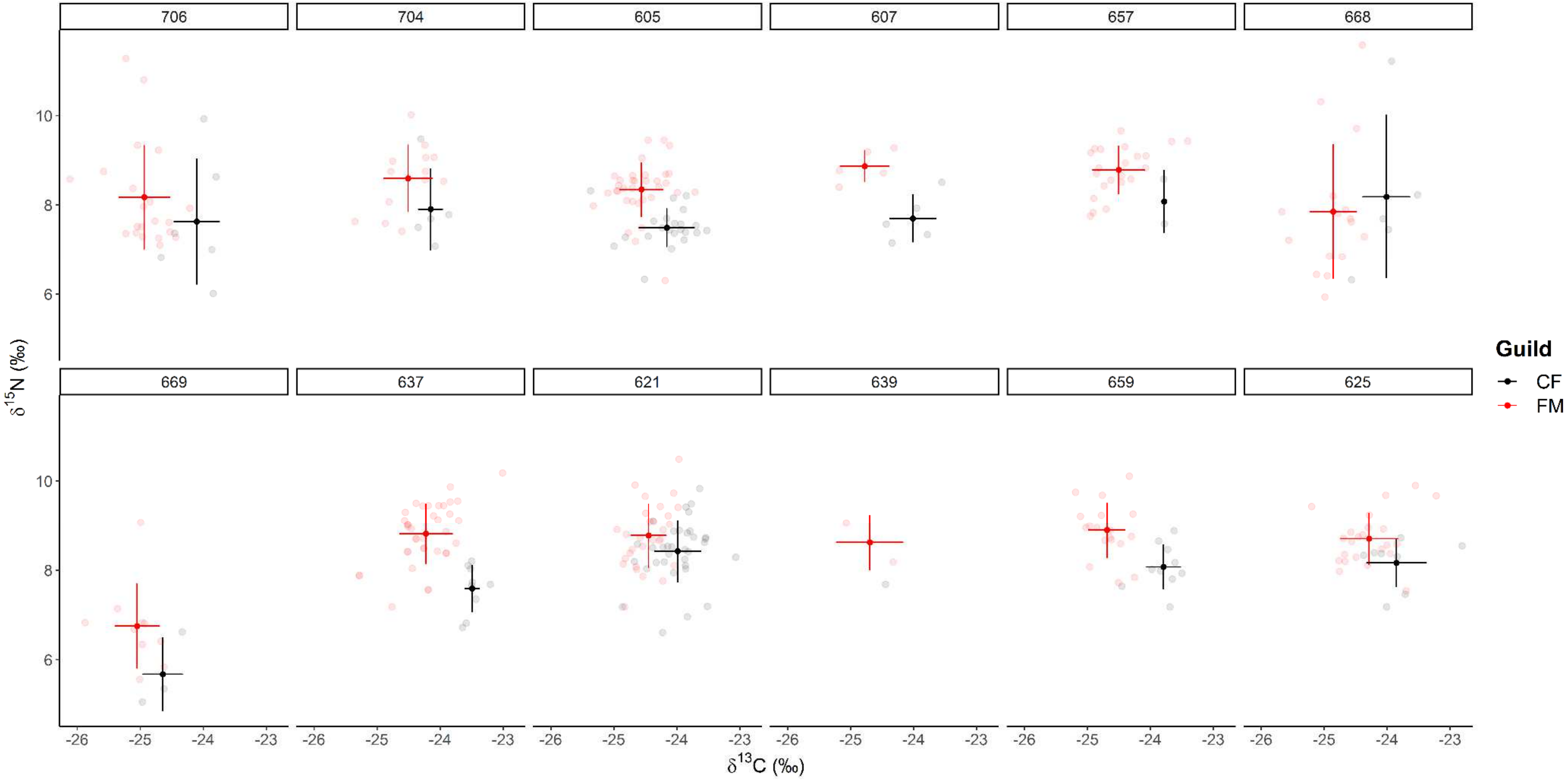


Figure 3.5. Differences in mean isotopic composition between two echolocation guilds, across all sampling plot, ordered by decreasing % forest cover (1 km extent); top left to bottom to right. Feint circles show the raw data, *i.e.* individual bats, and solid circles show the guild-specific means. Red circles and lines represent low-duty-cycle (LDC) echolocation guild and black circles and high-duty-cycle (HDC) echolocation guild.

Discussion

By combining landscape-scale sampling of high-level predators over a gradient of forest degradation with established diet tracing analyses and newly-develop tools for isotope data analysis, I demonstrate how isotopic niches of mobile bat predators contract with reduced forest quantity, whilst population-level trophic positions decrease with improved local forest quality. I detected a strong dietary response, despite sampling a relatively homogenous landscape of twice-logged forest. By characterising both local- and landscape-scale environmental variables, I address the relevant spatial scale to use when studying different parameters of resource use for an assemblage of forest-interior bats. In contrast to dietary responses, I found biodiversity metrics to be unaffected by environmental characteristics. These results highlight the critical need to develop assessments of human impacts on ecological communities, which go beyond classic diversity metrics, and to consider multiple spatial scales (local and landscape).

Response of trophic structure to forest degradation

There was a positive relationship between landscape-scale forest cover and isotopic niche breadth for predators after accounting for species differences, indicating generality across dominant bat species. A moderate loss (~26%) of forest cover was associated with a strong reduction (78%) in predator's isotopic niche breadth.

Diet reconstruction for consumers based on their isotopic signature depends on the assumption that it averages prey isotopic signatures, weighted by their relative biomass contribution (Fry 2008). Bat predator signatures reflect relative contributions of prey taxa belonging to different feeding guilds. For instance, five insect orders were found to each contribute > 10% biomass to the diet of the tropical gleaning bat, *Micronycteris microtis* (Kalka & Kalko 2006); these orders represented a range of different feeding guilds that included herbivores, detritivores and predators (*e.g.*

Lepidoptera, Blattodea and Odonata, respectively). The niche contraction in our study likely reflects reduced diversity of basal resources and insect prey available to predators due to forest degradation. Although I did not directly test the mechanisms governing the observed patterns, tropical forest degradation is known to drive turnover of insect communities and alter predator-prey interactions (Tylianakis *et al.* 2007; Pellissier *et al.* 2017). Niche contraction could therefore reflect the shifts in the insect community composition and relative guild densities following the forest degradation. For example, a shift to dominance of insect communities by herbivores would reduce the diversity of basal resources flowing to upper trophic levels. In the Neotropics, bat species have generally been shown to adjust their diets to local changes in resource availability (Rex *et al.* 2010), although such alterations may be less pronounced in obligate insectivores. On the other hand, predator habitat use may have a strong influence on diet composition and resource breadth (Tunney *et al.* 2014), potentially independent of changes to prey community composition. A better mechanistic understanding of niche contraction processes requires experimental partitioning of direct effects of environmental change on predator habitat use and foraging behaviour, and indirect effects through changes in their prey community compositions.

Given that landscape-scale forest cover is positively associated with proximity to better quality forest patches (Ewers *et al.* 2011), I highlight two potential mechanisms which may have strengthened the correlation between landscape-scale forest cover and predator niche breadth. Firstly, insect dispersal from source populations in high quality forest might have maintained more diverse local prey assemblages (Laurance & Bierregaard 1997), and secondly wider-ranging bats may have foraged within these higher quality patches. In support of the latter mechanism, there is evidence for an interactive effect between insect abundance and landscape characteristics upon bat activity (Heim *et al.* 2017). Furthermore, inter-individual variation, to which population niche parameters are sensitive (Fink *et al.* 2012; Layman *et al.* 2012) can increase with environmental stability (Dermond *et al.* 2017). Thus, I would expect expanded predator niches in patches with higher forest cover, associated with more stable environmental conditions. In comparison, that I detected no effect of local habitat quality upon species' niche breadths indicates a weak association between the underlying mechanisms of niche contraction of these bat assemblages and characterisation of relatively narrow vegetation plots.

I have been able to capture to some extent the ^{15}N-isoscape of the forest sites, and substantial variation is evident amongst sites. I accounted for among-site differences in mean ^{15}N of basal leaf resources in the calculation of trophic position. There is also potential for altered variation in stable isotope baseline values to have cascaded to higher trophic levels, thereby altering isotopic niche width of predators independent of any modifications in diet composition. Although figure 3.3 indicates substantial among-site differences in the variation of leaf isotopic composition, potentially deriving from disturbance related changes to the forest, there is no correlation with predator niche width. In order to achieve truly baseline-independent conclusions, it would have been necessary to measure component-specific stable isotope ratios, e.g. in essential and non-essential amino acids. Finally, the duration of trapping campaigns among sites differed slightly due to variation in the local abundance of bats, which could have introduced inter-site differences in prey variability. However, as wing tissue integrates diet over more than four weeks (Roswag *et al.* 2014) this is unlikely to affect the isotopic niche breadth in comparison to results based on faecal or blood analyses. Moreover, the site ('F') with the lowest trapping intensity had the broadest isotopic niche for *K. intermedia*, a species dominant across the whole landscape, suggesting weak positive effects of trapping intensity on niche breadth.

Contrary to our prediction that reduced habitat complexity would result in shorter food chains (Fig. 3.1), I detected an increase in mean trophic position with decreasing local canopy height (Fig. 3.2B). This was surprising given that lower canopy height is typically associated with reduced forest complexity, and thereby reduced proportional abundance of arthropod predators (that include both insects and non-insects). For example, Denno et al., (2005) showed that less complex habitat hosted lower densities of predatory insects, which they attributed to the lack of refuge from intra-guild predation as well as fewer insect prey and reduced foraging efficiency. Others have also shown that direct impacts of land-use change on insect predators tend to be stronger and more negative compared to the relatively weak impacts on other trophic guilds such as insect omnivores (Barnes *et al.* 2017), thereby likely reducing the ratio between arthropod predators and primary consumers. Although generally assumed that trophic position decreases with degradation, previous studies show an increase (Woodcock *et al.* 2013) or no change (Nakagawa *et al.* 2007) in trophic position of terrestrial taxa with habitat degradation.

Recent theoretical predictions are consistent with our results: they showed that, counter to classical hypotheses, ecosystem productivity can negatively affect food chain length through shifts toward increased omnivory (Ward & McCann 2017). High productivity across our study system, secondary lowland forest, is likely to be the principal driver of trophic omnivory (Ward & McCann 2017). Considering that the most degraded sites have the lowest levels of productivity, and that productivity has a negative effect on omnivory then I would expect food chain length, and therefore predator trophic position to be higher at the degraded sites.

An alternative explanation for our finding that bats appear to rely more on arthropod predators in degraded forest is that there may be a greater availability of parasitoids. These specialised predators may represent a significant fraction of non-herbivore insects in the forest interior as parasitism rates for most insect herbivores typically range between 5 to 40%, and the ratio of parasitoids to hosts tend to increase with the degree of habitat modification (Tylianakis *et al.* 2007). However, we still have a limited understanding of how physiological and environmental factors influence bioaccumulation of ^{15}N (review by Martinez del Rio et al. 2009), processes that can affect the accurate estimation of trophic position. These processes warrant further investigation, and combination of multiple diet tracing methods (Nielsen *et al.* 2018) could provide more direct evidence on the contribution of specialised parasitoids to the diets of aerial insectivores.

There is likely considerable variability in $\delta^{15}N$ values among plants which are present at our sample sites (Craine *et al.* 2015) due to variable life histories. There is potential for this to introduce noise to the plot-specific nitrogen baselines given that taxonomic representation was not consistent. By averaging values from abundant morphotypes of plant from each plot, I hoped to minimise effects of such variation (See supplementary Table S3.3 for mean values). I made every effort to minimise noise in the baseline values, for example time-matching to collection of bat tissue samples. Ideally I would have reported compound specific $\delta^{15}N$ ratios of amino acids in the bat tissue to extract trophic position (Chikaraishi *et al.* 2009), however I focused my budget on intensive sampling of bats, to address their ecology across a landscape scale.

The finding of an echolocation-specific shift across isotopic space, with HDC echolocators significantly enriched in ^{13}C and depleted in ^{15}N compared to LDC echolocators (Fig. 3.5), supports previous evidence of inter-guild niche partitioning within assemblages of echolocating bats (Denzinger *et al.* 2016). I also found marked inter-guild differences in trophic position, independent of sampling location. The relatively lower trophic position of HDC echolocators is supported by their description as flutter-detection specialists (Jacobs & Bastian 2016), indicating a high dietary intake of mostly herbivorous Lepidoptera. Inter-guild differences in trophic position were not affected by habitat degradation.

The two echolocation guilds differed in their mean isotopic niche breadth, even after accounting for sampling location. Furthermore, HDC echolocators responded more strongly to gradients of local quality compared to LDC echolocators (Fig. 3.4). This result was not expected, however, it is known that some cave roosting HDC bats are able to forage over several hundred metres (Rossiter *et al.* 2012). Therefore, it is possible that isotopic signatures of these bats aggregate resources across areas which more closely match the spatial scale over which habitat quality varies. When considering larger scale differences in forest degradation as a result of selective logging*, i.e.* > 1 km, I did not see any differential response in the niche breadth of echolocation guilds. At this scale, differences in echolocation type among bats may be less important determinants of diet than other traits such as home range (for these bats < 100m up to > 2 km). It is likely that there would be greater variation in the response to habitat degradation among foraging guilds, as classified by Denzinger and Schnitzler (2013), which are assigned to maximise shared temporal, spatial, food-specific and environmental niche dimensions. I make the assumption that vegetation plots are representative of the habitat in which they are embedded, *i.e.* in which focal bats are living and foraging. I argue that although 25m^2 plots are smaller than the range of focal bat species, they are reasonably reflective of both large-scale (based on terrain, and locations of logging roads etc.) and small- scale (extraction quantity of large trees) disturbance in the area.

Stability of guild niche locations was observed irrespective of habitat type (Fig 3.5). The pronounced differences in carbon isotopic composition between bat guilds indicate that carbon resource breadth may play an important role in the observed inter-guild differences in niche contraction, as postulated in other studies (Layman, *et al.*, 2007). A promising avenue for further work is estimation of the dietary contribution of different carbon resources, channelled to predators via their insect prey (Parnell *et al.* 2013; Perkins *et al.* 2018). It seems likely that low quality forests support food webs with increased dependence on fewer basal resources. For example, bats could be feeding on equal prey species diversity across the degradation gradient, but those prey are dependent on less diverse basal resources, thereby reducing the range of carbon signals propagated through the food chains. The marked niche contraction in our study was associated with increased grass cover, and dominance of *Imperata cylindrical.* This grass species invades and dominates human-modified forest areas, as the prevailing basal resource, but is likely a low quality resource.

Conclusions and applications

I took advantage of an established gradient in the severity of forest degradation as a result of selective logging, which allows us to look at medium-term effects of this process of timber extraction. The changes in isotopic niche dimensions could be a temporal phenomenon, perhaps re-establishing to the pre-logging situation given time. However, I observed very strong effects after a period of approximately 30 years post logging, and believe that there may be even stronger effects in the longer term. Indeed, regardless of the future direction of change, it is very important and interesting to understand these transient dynamics in the system.

The early effects of habitat degradation are likely to be apparent through dietary shifts and niche contractions, which may reduce persistence and stability of populations and communities (Rooney *et al.* 2006; Kratina *et al.* 2012a). For example, compression of the isotopic niche under landscape homogenization, and reduced interspecific partitioning of resources, has been linked to intensified competition between resilient species (Manlick *et al.* 2017). The mean forest cover in our sampling locations was far above the threshold (30% cover) above which community composition of vertebrates often remains intact, as judged from a large-scale multi-taxa field study (Banks-Leite *et al.* 2014). Indeed, the bat community composition was not affected over the gradient of habitat degradation in our study area. The strong dietary response to minimal degradation of mature secondary forest complements studies suggesting that that functional trait composition (Hector *et al.* 2011; De Coster *et al.* 2015) and trophic interactions (Tylianakis *et al.* 2007) differ from species richness and species composition in their responses to forest degradation.

Observed changes in predator diet reveal altered biotic interactions, and associated ecosystem functions, which are uncoupled from changes to predator community composition. The ability to generalise as to how ecosystem functions, such as energy flow and nutrient cycling, will respond to local disturbance is critical to management strategies and policies. Detailed understanding of these changes can improve predictions for future impacts of large scale land use on ecosystems, and aid in establishing thresholds of habitat quantity and quality above which ecosystem functioning remains intact. This is particularly important in tropical forests which provision countless natural services and products, signposted by their high priority focus in the context of the CBD 2020 targets for Biodiversity (Convention on Biological Diversity 2012). I conducted this study in Sabah, Borneo, which alongside Sumatra, experiences the highest loss of forest covering Southeast Asia (Stibig *et al.* 2014). In Sabah the conservation battleground concerns secondary forest as all primary forests are fully protected, which makes our findings directly relevant to policy and land management. Based on our results I argue that patches of secondary forest with forest cover above 90% should be prioritised for conservation over more highly degraded land in order to maintain integrity of ecosystem functions and services.

Supplementary Methodology (Chapter 3)

S3.1. Sample weights of biological materials

Bat wing punches weighed 0.0174 to 0.1161 mg (mean 0.0595; SD 0.0145). Reported sample weights are after removal of large weights indicative of contamination, or very low beam area (<9.99e-09). Living leaf samples were weighed to 4.9069 to 5.187 mg (mean 5.0923; SD 0.0587).

S3.2. High precision set-up of the elemental analyser

For analysis of the bat wing punches we pioneered a high-precision set up of the CF-IRMS (Sercon, Crewe, UK). Chemical reagents normally housed in separate combustion and reduction reactor columns were combined into a single reduced-volume reactor column in order to maximise efficiency in the conversion of the solid sample material into those gasses which will be analyses (N_2 and CO_2). Precision test using Protein (Casein) Standard OAS (Elemental Microanalysis, Okehampton, UK) gave a standard deviation 0.2 ‰ for N_2 (^{15}N) (80µg, *n=4*). The sample weight equates to approximately 10 µg of Nitrogen (certified % Nitrogen is 13.32). Linearity test using dried urea samples gave a standard deviation of 0.258 ‰ for N_2 (^{15}N) *(5, 6, 12, 15, 18 µg; n=1 for each increment)* across the range of nitrogen elemental content for wing punch samples included in this analysis (5-20 µg). This compares to specified precision of 0.3 ‰ (100 µg, n=5) in standard operating set up.

S3.3. Quality control of bat wing tissue delta values

I removed six bat wing data points due to a very low ^{15}N beam area. These were either due to very low sample weights (<0.03 mg) or, when falling in the viable weight range, due to analytical error. A further 7 data points were removed as the analysed sample could not be matched to the original field data and therefore remained unallocated to a population.

S3.4. Accuracy of isotopic measurements

In order to assess accuracy of isotopic measurements on bat wing tissue and leaf material, I calculated the mean and standard deviation of isotopic measurements on casein IRMS standard.

material	caesin mean	caesin SD	n
Wing tissue	5.909	0.352	114
Leaf	5.975	0.708	14

S3.5. Autocorrelation in mixed effects models

I fit mixed effects models testing Bayesian standard ellipse area (SEA_b) and trophic position, including a number of different spatial autocorrelation functions into the random component of the models using GPS coordinates of the plots. Since the correlation structure cannot handle zero distances between observations, and we had multiple observations per plot, we made a change (< 0.01) to the longitude for the coordinates associated with each unique combination of species and plot. The correlation functions we tested were: exponential, Gaussian, linear, rational quadratic and spherical. We compared models without and with different autocorrelation functions using the Akaike's Information Criterion (AIC). There was no significant difference in AIC values (Table S3.4) among these models so we present results from models without autocorrelation structure. Furthermore, for significant relationships between the response and explanatory variable, we also plotted the unexplained variance in the model (normalized residuals) against the geographic distance between observations in order to detect signs of spatial structure in the residuals (supplementary Fig. S3.2).

Supplementary Tables (Chapter 3)

Table S3.1 Environmental characteristics for each plot.

Environmental variable	Site/Plot												Number of plots
	LFE		F		E		D		C		B		
	704	706	668	669	657	659	637	639	621	625	605	607	
Forest cover over 1 km extent (%)	94	96	86	84	86	80	83	81	81	74	87	87	12
Forest cover over 1.5 km extent (%)	92	92	77	76	80	73	82	80	73	58	86	88	12
Biomass	90.01	189.43	76.28	136.77	51.06	69.16	67.91	39.01	NA	15.43	62.34	113.38	11
Canopy height (m)	21.75	32.54	21.82	35.48	3.89	31.28	9.55	5.17	1.29	15.73	21.05	5.69	12
Mean proximity to stream (m)	67	125	248	128	448	721	6	237	607	810	116	50	12
Tree Cover (%)	40	30	70	50	NA	NA	NA	NA	25	10	30	50	8
Grass Cover (%)	5	5	0	0	NA	NA	NA	NA	10	45	20	10	8

Table S3.2. Modal standard ellipse area and mean trophic position for bat populations. Here, populations are defined as conspecific individuals captured at harp trap locations which have in common their relative proximity to a sampled vegetation plot. Sample numbers are in brackets following the estimates of dietary metrics. Grey entries represent < 5 individuals and therefore unique combinations of Species identity and plot which were excluded from analyses.

Site	Plot	LDC guild				HDC guild			
		Kerivoula intermedia		*Kerivoula hardwickii*		*Hipposideros cervinus*		*Rhinolophus trifoliatus*	
		Modal SEAb	Mean TP	Modal SEAb	Mean TP	Modal SEAb	Mean TP	Modal SEAb	Mean TP
LFE	704	0.742 (10)	4.112 (10)	(3)	(3)	(2)	(2)	(2)	(2)
	706	0.612 (14)	3.346 (14)	2.591 (7)	3.435 (7)	(3)	(3)	(3)	(3)
F	668	1.496 (10)	3.576 (10)	1.390 (6)	3.540 (6)	(4)	(4)	(1)	(1)
	669	0.491 (8)	3.436 (8)	(2)	(2)	(1)	(1)	(2)	(2)
E	657	0.476 (12)	3.868 (12)	0.543 (10)	3.992 (10)	(1)	(1)	(1)	(1)
	659	0.258 (9)	2.955 (9)	0.464 (9)	3.049 (9)	0.096 (5)	2.856 (5)	0.265 (5)	2.664 (5)
D	637	0.682 (24)	3.898 (24)	0.548 (13)	4.038 (13)	(0)	(0)	0.136 (9)	3.586
	639	(1)	(1)	(1)	(1)	(0)	(0)	(1)	(1)
C	621	0.449 (18)	3.495 (18)	0.324 (11)	3.566 (11)	0.492 (27)	3.493 (27)	0.702 (7)	3.136 (7)
	625	0.511 (10)	3.856 (10)	0.846 (13)	3.859 (13)	0.045 (5)	3.775 (5)	(3)	
B	605	0.483 (6)	3.136 (6)	0.382 (7)	3.190 (7)	0.456 (13)	2.966 (13)	0.441 (9)	2.832 (9)
	607	(1)	(1)	(4)	(4)	(4)	(4)	(1)	(1)

Table S3.3. Sample numbers and mean ^{15}N values for C_3 leaves collected at each plot. Sample mean ^{15}N values were used for $\delta^{15}N_{base}$ in the calculation of trophic position.

Site	Plot	C3 Leaves	Mean ^{15}N	SD ^{15}N
LFE	704	13	-2.04	1.23
	706	9	0.10	1.83
F	668	10	-0.86	1.9
	669	16	-1.59	1.75
E	657	13	-1.15	1.92
	659	5	2.09	1.68
D	637	15	-1.21	2.18
	639	16	-0.89	2.15
C	621	14	0.20	2.59
	625	6	-1.01	1.97
B	605	11	0.99	1.86
	607	18	-0.45	1.6

Table S3.4. Comparison of candidate mixed effects models with different spatial autocorrelation classes fit with function lme in package *nlme.* Values of Akaike's Information Criterion (AIC) are given for models of Bayesian standard ellipse area (SEA_b; long transformed) and trophic position (log transformed) as response variables. The best model (lowest AIC) is highlighted in bold print.

corStruct class	**Autocorrelation type**	**AIC SEA_b**	**AIC trophic position**
none	NA	**67.901**	**-26.378**
corExp	exponential spatial	69.244	-24.442
corGaus	Gaussian spatial	69.244	-25.027
corLin	linear spatial	69.244	-24.780
corRatio	rational quadratics spatial	69.244	Failed to converge
corSpher	spherical spatial	69.244	-24.377

Table S3.5. *P*-values for the interaction term (echolocation guild as the covariate) and main effect of environmental predictor variables on modal SEA_b and mean trophic position. Grey represents non-significance.

Response	Predictor	Main effect	Interaction	n
SEA_b (log)	Forest cover (1 km)	0.0022	0.0654	26
	Forest cover (1.5 km)	0.0274	0.1411	26
	Mean proximity to stream	0.0414	0.7782	26
	Biomass	0.0109	0.0919	22
	Canopy height	0.8223	0.1389	26
	% Trees	0.0098	**0.0114**	17
	% Grass	0.0076	**0.0151**	17
Mean trophic position	Forest cover (1 km)	0.981	0.225	26
	Forest cover (1.5 km)	0.588	0.315	26
	Mean proximity to stream	0.432	0.731	26
	Biomass	0.434	0.106	22
	Canopy height	0.002	0.523	26
	% Trees	0.741	0.027	17
	% Grass	0.41	0.432	17

Table S3.6. Model comparison using anova F statistic of models including and excluding the interaction term. Comparison has been conducted for those models with a significant interaction term between the main effect and the covariate.

Model	F value	P-value
$LogSEA_b$ ~ % Tree Cover * Guild $LogSEA_b$ ~ % Tree Cover + Guild	8.6808	**0.011**
Log SEA_b ~ % Grass cover * Guild Log SEA_b ~ % Grass cover + Guild	7.8326	**0.015**

Supplementary Figures (Chapter 3)

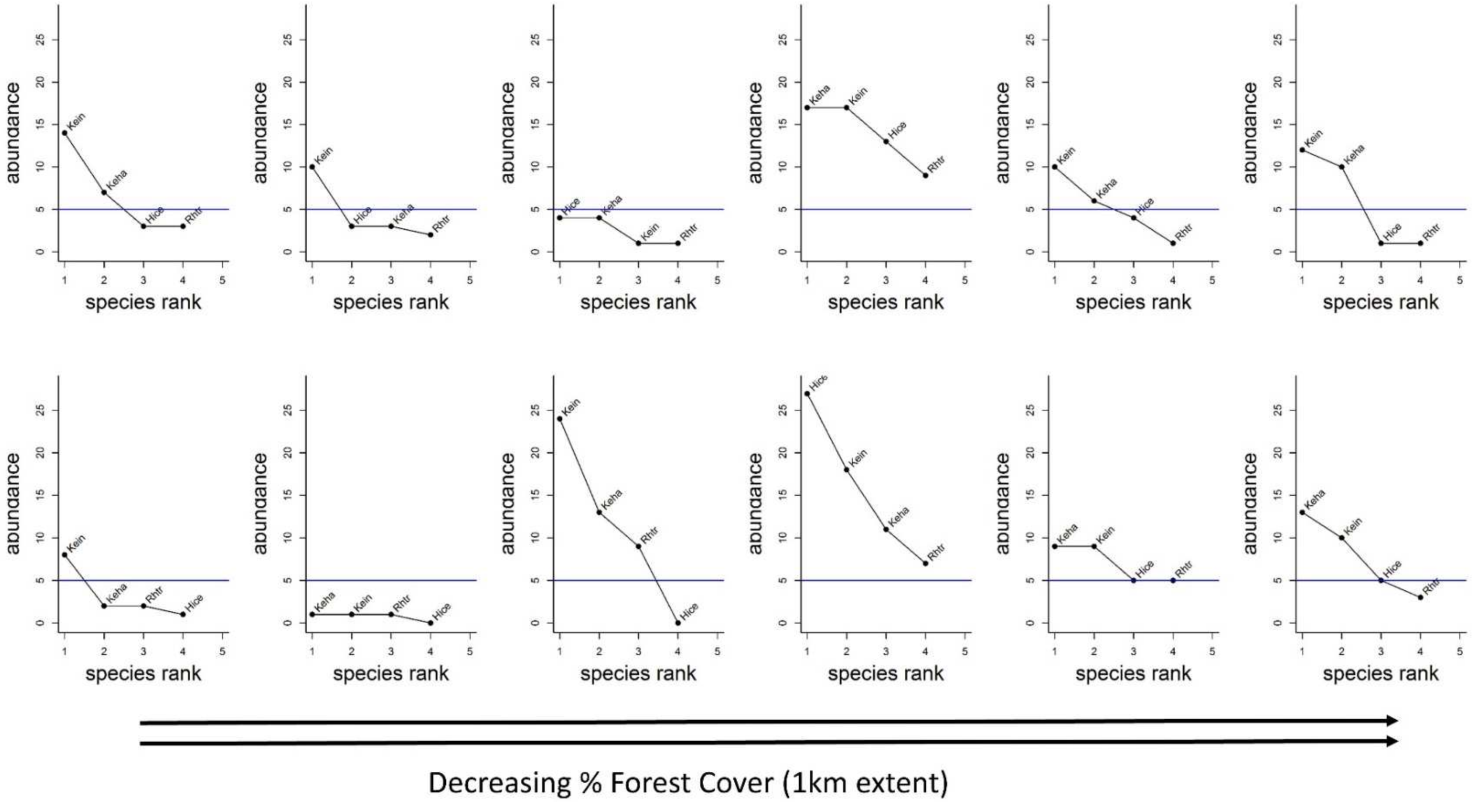


Figure S3.1. Species rank abundance at each plot, with the blue line (abundance = 5) indicating the threshold below which populations are excluded from analyses due to statistical constraints of calculating modal standard ellipse area (SEAb). Plots are ordered by increasing percent forest cover at the 1 km extent.

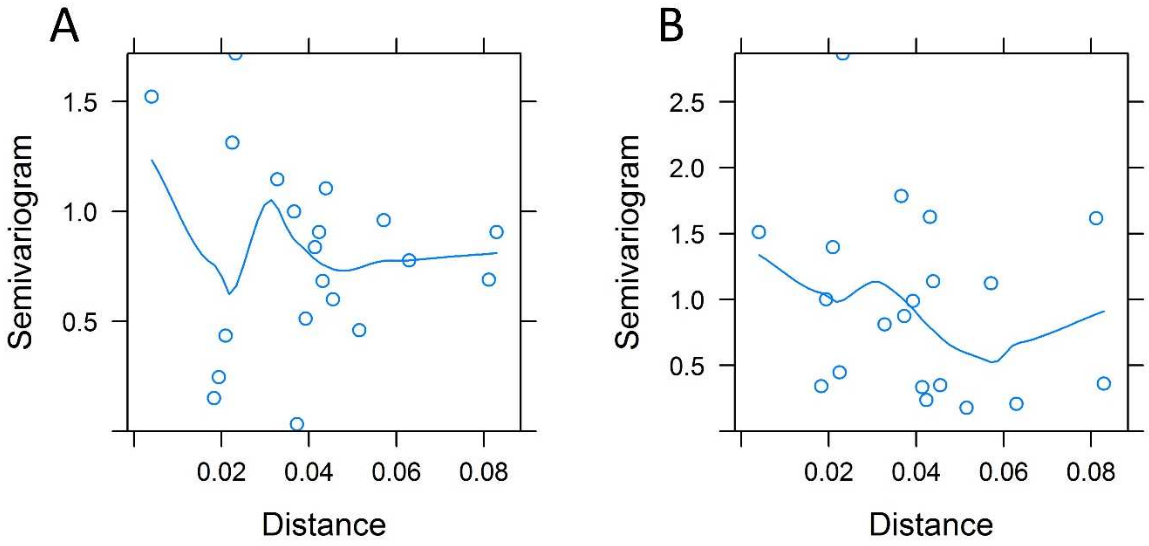


Figure S3.2. Plots of the unexplained variation in the data (residuals) against geographic distance between observations. Each dot is a residual from the fitted model, and the blue line is the smoothed relationship between the unexplained variance and geographic distance between observations. Variograms of [A] SEA_b (log) by forest cover (%; 1 km), and [B] trophic position (log) by canopy height (m).

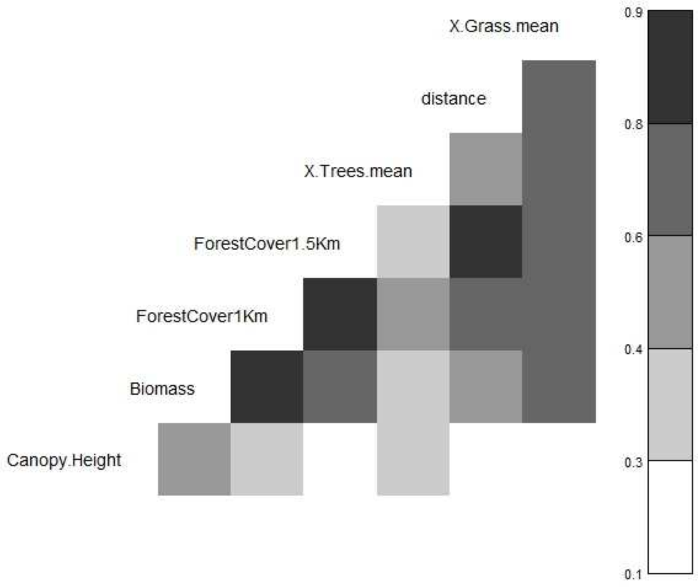


Figure S3.3. Collinearity plot of all explanatory variables which were include in the analysis, indicating the relatedness between different variables. We use a threshold of 0.6 to include multiple variables, *i.e.* not strongly correlated.

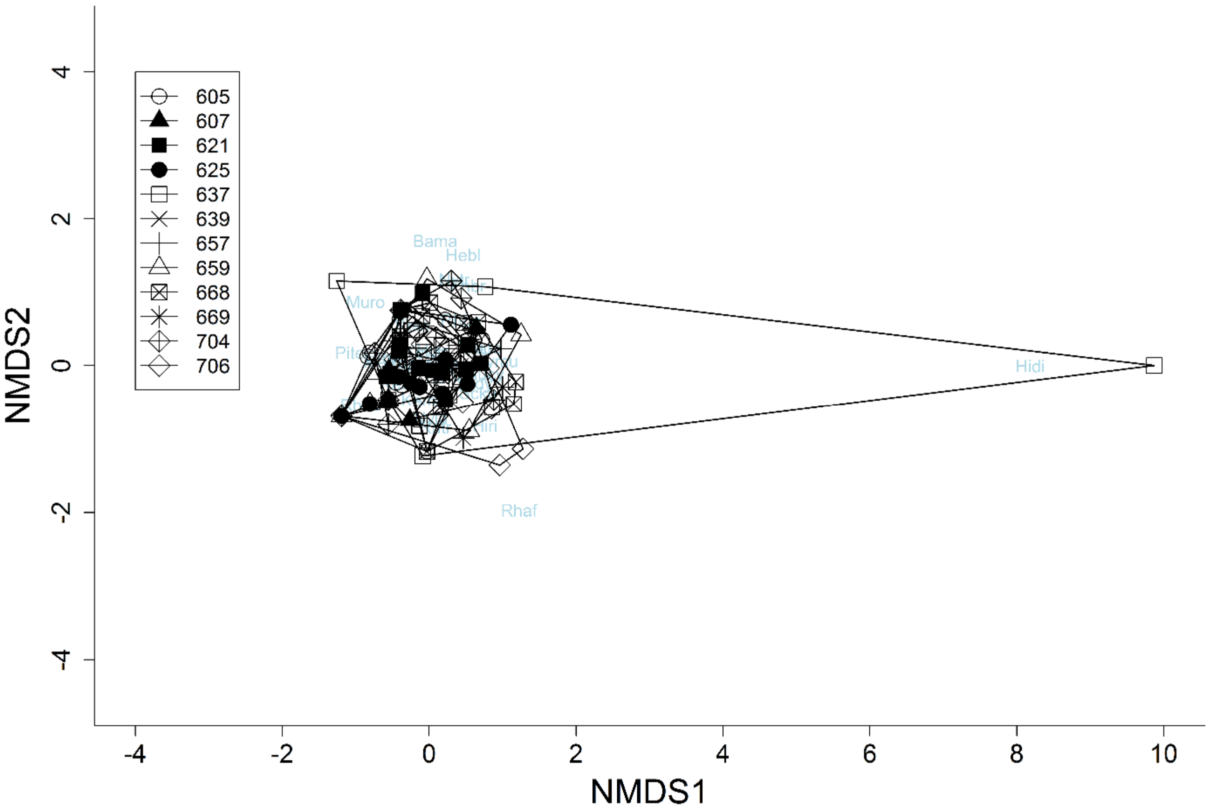


Figure S3.4. Non-metric multidimensional (NMDS) representation of species abundance by sample plot. Average community measures are shown as large symbols with contours drawn around communities from the same plot. [Total n = 12]. Communities are based on a matrix of trap-level raw species abundance [species n = 30, trap n = 145], and species are coded by four-letter binomial names in light blue. Stress = 0.09, linear fit r^2 = 0.012.

CHAPTER 4

Interannual variation in the impacts of post-logging habitat simplification on resource use of abundant bat predators

Bat captures, Maliau Basin Conservation Area

Abstract

Given extensive conversion and structural simplification of tropical forests, there is an urgent need to understand the value of degraded forest for biodiversity and provision of ecosystem services. Regenerating forests remain structurally distinct from their primary counterparts decades after logging disturbance, with potential impacts upon ecosystems which are more pervasive than alteration to species diversity. I employed stable isotope analyses to investigate shifts in food web structure cross a gradient of forest vertical structural complexity. At the extremes of this gradient were regenerating forests, approximately 30 years since logging, and old-growth forest. I determined differences in food web structure using data collected over a three-year period, and compared long-term (multidecadal) alterations to trophic interactions with shorter-term (1-2 years) responses to an El Niño drought event. Furthermore, I addressed the severe knowledge gap regarding the interactive effects of logging impacts and climatic effects. I predicted that structurally simplified, regenerating forest would be associated with reduced resource availability for insectivorous bats, leading to reduced niche breadths of bat assemblages, decreased trophic position due to simplified food chains, and reduced trophic redundancy due to competition-driven specialisation. Resource use by assemblages differed across the spatial gradient of habitat complexity, with the carbon stable isotope ratio measured on wing tissue of abundant bat species increasing in less complex forest. There were stronger interannual responses than expected, suggesting that food web structure and dynamics can change over short time frames even in tropical environments. Decreased habitat complexity and short-term drought stress appear to be additive, and synergistically they enrich bat predator $\delta^{13}C$ values by approximately 3.5‰. Increased dependence of bat assemblages upon ^{13}C-enriched resources could reflect greater dependence on detrital

resources, with substantial potential to affect the asymmetry between food web compartments and decrease resilience to future perturbations.

Introduction

Globally, tropical forests have experienced conversion and degradation for purposes of timber extraction and agricultural expansion (Laurance et al. 2014; McRae et al. 2014), and these pressures show no signs of abating (Potapov et al. 2017; Hughes 2018). Tropical ecosystems provide myriad critical goods and services to the World's poorest communities (Bradshaw *et al.* 2009; Cardinale *et al.* 2012), as well as globally important ecosystem services including sources of new medicines and climate regulation (Foley *et al.* 2007). Despite persistent pressure to these areas of high value, the extent to which habitat degradation influences biotic interactions (Barnes *et al.* 2017) and food web structure and energy flows (Woodcock *et al.* 2012; Edwards *et al.* 2013) has received minimal attention.

Regenerating forests tend to have reduced structural complexity compared to their primary counterparts (Okuda *et al.* 2003; Asner *et al.* 2009; Rutten *et al.* 2015), with potentially negative consequences for multiple ecological parameters such as habitat diversity (Tews et al. 2004) and spatial heterogeneity (Kitching et al. 2013). As expected, there is strong evidence that biodiversity in logged forests is reduced when compared to primary forest (Meijaard et al. 2006; Gibson et al. 2011), however post-logging impacts on the forest ecosystems may be more subtle than alteration to species diversity. For example, trophic interactions may be altered as a result of changes habitat availability and obstacles to animal movement associated with local and landscape vegetation structure. Furthermore, alterations to stand physical and community structure in regenerating forests influence key ecological processes which govern nutrient cycling and productivity (Denslow 1987; Prescott 2002; Riutta *et al.* 2018), with potentially large effects upon food-web structure and dynamics (Edwards et al. 2013; Woodcock et al. 2013).

Vegetation structure is closely associated with habitat suitability for species from all trophic positions, thus influencing species interactions, food web structure and ecosystem function. For example, changes to leaf and twig density at multiple vertical levels can affect community assembly of tropical birds (Ansell *et al.* 2011) and mammals (Cusack *et al.* 2015). This agrees with theoretical explanations that increased structural complexity provides more niches (habitat heterogeneity hypothesis; Simpson 1949), and empirical observation of increased species diversity with structural complexity (Tews *et al.* 2004). Other components of vertical complexity, such as top-of-canopy height are also good predictors of habitat suitability for birds, mammals and insects (reviewed in Bergen *et al.* 2009). Thus the impacts of vegetation structure on whole community assembly and consumer habitat use should effect trophic interactions, and alter resource use and feeding behaviour of forest consumers in post-logging forest (Edwards *et al.* 2013; Müller *et al.* 2013).

Bats are the most ecologically diverse mammals in the tropics (Dammhahn & Goodman 2013) and are characterized by high local abundance; species richness, and trophic diversity, representing distinct major feeding guilds (Kalka & Kalko 2006). A number of studies have found 3-D vegetation structure is well correlated with habitat use for bats, when assessing vegetation with both ground-based (Dodd *et al.* 2012) and remote-sensed methods (Müller *et al.* 2013; Blakey *et al.* 2017). Moreover, vertical forest structure has been shown to affect fine-scale bat foraging behaviour in terms of flight trajectories (Yang *et al.* 2013). Such changes to habitat use and activity will likely restrict the insect prey which are available to bats. Resource use can also be impacted by indirect effects of habitat change that alter prey availability. Degraded forests host distinct insect communities to primary forest (Lawton *et al.* 1998; Barlow *et al.* 2007; Tylianakis *et al.* 2008). Changes to insect communities are likely driven by a combination of top-down control (Kalka & Kalko 2006) and bottom-up processes (*e.g.* plant-hosts available locally to larvae; Kitching *et al.* 2013). Insect communities are likely highly affected by altered alter environmental conditions such as temperature, humidity and soil moisture as a result of canopy gaps following logging, i.e. from extracted and dying trees, which expose the forest floor (Jucker *et al.* 2018a). As highly mobile predators, pursuing areas of concentrated prey source (Wickramasinghe *et al.* 2004; Kalcounis-Rueppell *et al.* 2007), insectivorous bats are likely to reflect both local and landscape-scale logging impacts in their behaviour and diet composition. Insectivorous bat diet often incorporates distinct resource compartments ("multichannel feeders"; Wolkovich *et al.* 2014), which may have stabilizing effects on food webs (Rooney *et al.* 2006). Their behavioural responses to changes in their environment (*e.g.* habitat connectivity; LeCraw *et al.* 2014) can cause disproportionate changes to food web dynamics and stability (McCann *et al.* 2005; Bartley *et al.* 2018). Crucially, the study of bats can help inform upon the state of an entire ecosystem, including the effects of human alteration to the wider landscape.

Degradation of forests also has the potential to alter nutrient cycling within the system. Logging has the effect of altering expression of traits, from those which maximise tissue persistence and stability toward carbon capture and growth, with associated impacts for ecosystem processes with cascading effects to higher trophic levels (Both *et al.* 2018). In general, more productive ecosystems can support food webs with longer food chains (Post 2002a), likely driven by increased trophic richness (Post & Takimoto 2007). Lower net primary productivity in regenerating forests also tends to decrease litter inputs (Riutta *et al.* 2018). Decreased litter inputs are further reduced by a shift in canopy dominance from late-successional to early-successional species (Villela *et al.* 2006), given an increased consumption of primary resources, i.e. the leaves of early successional species are more palatable and consumed at much greater rates by herbivores (Denslow 1987). Altered taxonomic composition in the canopy also affects nutrient availability, for example N-fixing tree species have particularly nutrient rich leaves and thus where they are abundant they can greatly increase nutrient cycling (Prescott 2002). Such disturbance-related alterations to basal resources, *i.e.* resources for primary consumers and detritivores, can propagate up through food chains and alter food web architecture (Tunney *et al.* 2014).

Multichannel feeding, whereby consumers feed across distinct resource compartments, is common across different ecosystems (Wolkovich *et al.* 2014). For example, in primary tropical forest, both invertebrate and vertebrate predators depend on resources from both living-autotroph (green) and the detritus-based (brown) energy channels (Hyodo *et al.* 2010). Lower levels of litter input in regenerating forest could reduce omnivorous consumption from multiple resource channels (Wolkovich *et al.* 2014), and negatively affect ecosystem resilience (Recalde *et al.* 2016). Given that terrestrial consumers generally have less specialized, more omnivorous diets than freshwater consumers (Wolkovich *et al.* 2014), we could expect even stronger impacts in forest ecosystems. Reduced availability and diversity of basal resources could also lead to competition-driven niche differentiation of consumers (Resasco *et al.* 2018; Roeleke *et al.* 2018), thereby reducing trophic redundancy compared to communities in primary forest. Higher trophic redundancy, i.e. more species with similar trophic ecologies can increase resilience of rainforest communities to additional stressors as it provides protection against extinction cascades (Sanders *et al.* 2018) and enhances ecosystem functioning through interspecific facilitation (Cardinale *et al.* 2002).

Stable isotope values of representative individuals can determine the ecological (isotopic) niche of a species or functional group (Bearhop et al. 2004). Given that the an organisms' isotopic niche space implies its resource use, changes to niche parameters can reveal changes to degree of dietary specialisation (Broders et al. 2014), prey abundance (Jiménez et al. 2017) and resource access (Layman *et al.* 2007b). The axes of a species' isotopic niche are sensitive to habitat fragmentation (Layman *et al.* 2007b) and other environmental stressors (Reddin et al. 2016). Furthermore, quantitative analyses of carbon and nitrogen stable isotope data provide estimates of food-web characteristics (e.g. resource breadth, trophic diversity and trophic redundancy), closely related to resource use, degree of omnivory and resilience in terrestrial communities (Layman *et al.* 2007a; Newsome *et al.* 2007; Rader *et al.* 2016).

Here we employ stable isotope analyses to investigate changes in food web structure in regenerating forest, approximately 30 years since logging, compared to primary forest. We take advantage of a gradient of logging intensity, and resultant structural complexity to compare isotopic variation in major basal resources from the green and brown food web compartments, an assemblage of insectivorous bats and their insect prey. We also compare the length of the food chains and resilience-related food-web properties.

With an unprecedented dataset across three sample years, we aim to elucidate the community-level impacts of selective logging, and whether multi-decadal effects are consistent in the context of additional stressors such as climate change and human disturbance. We hypothesised that compared to primary forest, regenerating areas show: (i) shifts in resource availability, particularly driven by reduced litter input, reflected by enriched $\delta^{13}C$ values of bat wing tissue; (ii) lower $\delta^{15}N$ values of bats, as a consequence of diminished net primary productivity reducing trophic diversity; (iii) reduced isotopic variation of both insect prey and bat predators, due to contracted resource availability; (iv) decrease in trophic redundancy (less clumping in isotopic space) of bat assemblages, due to increased niche differentiation as resources becomes more sparse; and (v) large interannual changes in these metrics due to food web responses to El Niño drought. We aim to elucidate both the multi-decadal effects of logging, as well as short-term impacts from emergent environmental stressors upon changes to the food web structure and flow of energy through the ecosystem (Tunney *et al.* 2014; Antiqueira *et al.* 2017), with ramifications for healthy ecosystem functioning (Duffy 2003; Estes *et al.* 2011; Atwood *et al.* 2013). Importantly, we address a severe knowledge gap regarding the interactive effects of multiple stressors at a given location and time (Côté *et al.* 2016), focusing on the concert of local stressors and climate change (Barlow *et al.* 2018)

Methods

Study sites and habitat characterisation

I conducted fieldwork at the Stability of Altered Forest Ecosystems (SAFE) project in Sabah, Malaysian Borneo. Furthermore, I sampled at two primary forest sites: Danum Valley conservation area (DVCA) and Maliau Basin conservation area (MBCA). I sampled over three years, February – May 2015, March – July 2016, and May – July 2017, however only adding primary forest sites for the last two years. For each sampling site, I estimated a range of vegetation structure metrics (supplementary Table S4.4) in order to characterise local levels of forest degradation. I extracted vegetation metrics from raster layers generated from LiDAR data collected in November 2014 (Jucker *et al.* 2018b). I calculated site-specific mean metrics across grid cells within a 1 km buffer zone around the mean locations of successful harp trap positions, weighted by the number of bats caught in each trap across all years (supplementary Fig. S4.1). This method of extraction provided a consistent habitat assessment across all sites, and is well matched to the mean home range of insectivorous bat species in Borneo, *c.* 0.44 km^2 (Struebig *et al.* 2013).

Consumer and resource sampling and processing

I sampled bats, their insect prey and basal resources at eight sites in total, six logged sites within the SAFE experimental area and two primary sites approximately 400 km away. In 2015 I sampled all six sites within the SAFE experimental area. In 2016 I did not resample one of the repeatedly logged-forest sites ('F') for logistical reasons, but extended sampling to include primary forest sites Maliau and Danum. Within the SAFE experimental area, sample sites are located 2 to 7 km apart (Table 1.1), exceeding the mean home range of insectivorous bat species (Struebig *et al.* 2013). In each year, I performed ten nights of trapping using six four-bank harp traps set along existing trails at each site (total: 60 harp trap nights per site). I checked traps late at night and early the next morning (20.30 and 08.30), and moved them each day by at least 20m. For logistical reasons, site F was only sampled using 30 harp trap nights in 2015, and site LFE was sampled three times in 2015 due to low capture rates. On capture, I identified each bat to species and, for adult individuals, a wing membrane biopsy was taken using a 3mm punch (Schuco, Walford, UK) for stable isotope analyses and placed in separate tubes for same day processing. Heavily pregnant or recently recaptured bats were not sampled. All individuals were released at the point of capture. To characterise their community- and population-level diet use across a gradient of habitat disturbance, I focused on eight species which are generally abundant across the gradient. These species represent the families Hipposideridae, Rhinolophidae and Vespertilionidae (subfamily: Kerivoulinae). Within the Hipposideridae (leaf-nosed bats), I focused on the congeneric species

Hipposideros cervinus and *H. dyacorum*, and within the Rhinolophidae (horseshoe bats) on *Rhinolophus sedulus*, *R. trifoliatus* and *R. borneensis*. Within the subfamily Kerivoulinae (woolly bats), I studied congeneric bats *Kervivoula intermedia*, *K. hardwickii* and *K. papillosa*.

In order to determine the resources directly and indirectly consumed by bats, I collected their putative insect prey and primary basal resources at each site. These prey and basal resources were collected at two separate plots within each site (supplementary Fig. 4.1) in order to incorporate the variation across the foraging range of the bats. Across all three years, I collected samples of C_3 leaves and leaf litter (*i.e.* avoiding epiphytes and grasses), two of the major resources at the base of the food chain representing the green and brown food web compartments, respectively. Understorey C_3 leaves and freshly fallen litter samples comprised of ten morphospecies of woody plant, living and fallen, respectively. Morphospecies of living leaf and leaf litter were stored individually in cloth bags inside a drying cabinet maintained at 60°C. In 2017 only, I collected additional putative resources at each plot: dead wood, soil, C_4 *Imperata cylindrical* and freshwater algae. I collected dead wood from two distinct trees at each plot; for soil the top 2.5 cm was taken from two locations a minimum of 1 m apart using an auger of diameter 3 cm, and two samples of freshwater algae from different rocks were collected at the nearest streams or tributaries to the plots. For insect collection, I exposed one top- and bottom-collector Malaise trap containing soapy water for 48 hours at each of the two plots within each site. Subsequently, I assigned insects to coarse feeding guilds (herbivores, detritivores or predators) based on the principle larval feeding source (Smith & Schmitz 2016; personal communications with Darren Mann and James Hogan, Oxford Museum of Natural History). I analysed approximately 150 insect samples for the purposes of this study. See supplementary Tables S4.3 & S4.3 for site-specific insect and basal resource sample numbers, respectively.

Stable isotope analyses

I analysed bat tissue, insect and basal-resource samples for stable carbon and nitrogen isotopes. All samples were dried at 60°C for a minimum of 48 hours (Hyodo *et al.* 2010) except for wing membrane samples (< 0.3 g wet mass), which I dried for 2 hours only. Insect and basal resource samples were ground to a fine powder using a ball mill (Retsch UK Ltd., Hope, UK). To account for variable lipid content, which influence carbon isotope ratios, I carried out free lipid removal for all insects (Perkins *et al.* 2013), thereby increasing the relevance of guild assignment by larval feeding ecology. I transferred 1-10 mg of ground arthropod sample to a 1.5 mL Eppendorf tube, and followed the method used by Logan et al. (*2008*), derived from Bligh & Dyer (*1959*) to remove the lipids. I then weighed all samples into 6 x 4 mm ultraclean tin capsules (Elemental Microanalysis Ltd., Okehampton, UK) using an ultra-microbalance (± 1μg; Mettler-Toledo, Greifensee, Switzerland) to provide sufficient elemental carbon and nitrogen for analysis by continuous flow isotope ratio mass spectrometry (SERCON, Crewe, UK). I pooled insects by feeding guild to reach 1 mg sample weight where required. Due to their low mass (total N content of ~ 7μg), bat tissue samples were analysed in low volume reaction tubes within the elemental analyser to maximise solid to gas conversion efficiency, and I amended operating settings accordingly (see supplementary methodology 3.2). Isotope ratios are expressed in per mil (‰) relative to international reference standards ($R_{standard}$), which are Atmospheric Nitrogen and Vienna PeeDee Belemnite (VPDB) for nitrogen and carbon, respectively. For quality control of isotope values of bat wing tissue see supplementary methodology 4.1. To correct bat isotope values for a blank effect, I used a mass balance weighted mean equation to solve for the $\delta^{15}N$ value of the blank (Fry & Brand 1992), inputting data from a nitrogen dose series spanning beyond the breadth of nitrogen content in predator tissue (5 to 73µg). I used C_3 understorey leaves as an essential baseline for accurate calculation of predators nitrogen value (Post 2002b), which accounts for both temporal (Craine *et al.* 2015) and spatial (Ponsard & Arditi 2000) changes in ^{15}N associated with local nitrogen inputs (Woodcock *et al.* 2012). Local ^{15}N baselines were strictly time-matched to predator isotope samples, which accounts for enriching effects of aridity upon $\delta^{15}N$ of terrestrial predators sampled during relatively dry months and years (Popa-Lisseanu *et al.* 2015).

Statistical analyses

All statistical analyses were performed using the language environment R version 3.5.1 (R Development Core Team 2018). I used the R package SIBER to calculate four characteristics of insectivorous bat communities using the mean carbon and nitrogen stable isotope ratios for all abundant bat insectivorous bat species present at individual sites (for site-specific abundance see supplementary Table S4.1): range in (i) nitrogen ($\delta^{15}N$) and (ii) carbon ($\delta^{13}C$) stable isotope ratios, reflecting the complexity of trophic structure and variation in basal resources, respectively, (iii) mean nearest neighbour distance (Euclidean; MNND), indicating the resilience of the food web to environmental change through trophic redundancy (larger values indicating decreased species density and therefore impaired trophic redundancy); and (iv) standard deviation of the nearest neighbour distance (SDNND), indicating the evenness of species proximity within communities, providing an additional estimate of food web stability (Layman *et al.* 2007a). I also estimated the isotopic variance of predator bat species populations, putative prey (insects) and basal resources representing the green and brown food channels, fresh leaves and leaf litter, respectively. The multivariate, ellipse-based metric (SEAc, ‰^{2}) provides an estimation of 40 % of the isotopic variance within a group, and is robust to small sample sizes (Jackson *et al.* 2012). For insects and basal resources, I calculated variation within groups, trophic guilds and resource type, respectively. For predator populations, I analysed isotopic values between conspecific individuals, thereby the ellipse represents the species' isotopic niche, highly correlated with the species isotopic niche (Newsome *et al.* 2007).

Moreover, I calculated trophic position and mean carbon ($\delta^{13}C$) stable isotope ratios for each bat population. To calculate the mean trophic position for the eight dominant predator species per site, I used the equation with non-baseline-corrected nitrogen values for bats:

$$\text{Trophic Position} = 1 + (\text{bat wing } \delta^{15}N - C_3 \text{ plant}\delta^{15}N) / 3.4, \qquad \text{(eq. 1)}$$

where 1 represents the trophic position of C_3 plants at a site, and 3.4 the $\delta^{15}N$ enrichment per trophic level, $\Delta\ \delta^{15}N$ (Post 2002b). For all response variables I only retained species, feeding guilds or basal resource types which were well represented at a site. I used the threshold of 5 individual samples as this is the minimum requirement for SIBER analyses (Jackson *et al.* 2012). All these metrics were calculated at the site level, to yield single site-based estimates. See supplementary tables S4.6 – S4.9 for estimated metrics.

I analysed the impact of key characteristics of vegetation structure (see supplementary table S4.5 for descriptions), representing a gradient from primary to repeatedly logged forest. I conducted principal component analysis (PCA) to reduce the environmental dimensions, avoid multicollinearity between individual predictors and mitigate overfitting the regression model. For the PCA, I standardised all variables to prevent bias towards predictors that are dominant in absolute scale but perhaps not as relevant as other predictors in terms of effects upon the response. The principal component (PC1; Table 4.1) was used as a predictor variable of all food web metrics using linear mixed effects models (LMEs; Bates *et al.* 2015) in which; PC1 and year were fixed factors, as well as species identity in population-level analyses, and site identity was treated as a random factor. Model comparison and selection was carried out based on Akaike's Information Criterion to evaluate the fixed main effects and their interactions. The best-supported model was that with the lowest AIC and distinguished from similar models with ΔAIC < 2, or the most parsimonious model when undistinguished. Significance of each fixed factor was assessed using R package *lmerTest* (Kuznetsova *et al.* 2017; see supplementary tables S4.11 - S4.13 for AIC tables), employing Satterwaither approximation for degrees of freedom, which is considered more conservative than likelihood ratio tests (Luke 2017). When year was retained in the best model, and found to be significant I undertook pairwise comparisons to investigate between-year differences, and used Bonferroni correction to account for multiple tests in R package *multcomp* (Hothorn *et al.* 2008; supplementary table S4.15).

Results

Habitat characterisation

The PC1 axis explained 78.4 % of the among-site variation in the vegetation structure characteristics (Fig. 4.1, Table 4.1). Gap fraction (gf), kurtosis (kurt), skew and Moran's I for top-of-canopy height were all positively correlated with the PC1 axis, whereas all other variables were negatively correlated (Fig. 4.1). Given the high threshold for non-gap classification, > 10 m canopy height, an increase in vegetation density at any of the measured strata (except 2 – 10 m) should indeed decrease gap fraction. MBCA, C and D sites were very well represented by PC1, whereas site B was not well represented. Correlations were weaker with PC2 (explaining 12.2 % of the variation; Fig. 4.1, Table 4.1). There was more asymmetric contribution of variables to PC2, and the axis was predominantly driven by the density of understorey and midstorey vegetation. Plant area density horizons (0-70 m) largely separated based on strong positive correlations for all horizons greater than 30 m and weak negative correlations for all horizons below 30 m. The ecological interpretation of changes to these below-canopy strata is context-dependent: reduced understorey could be due to prevention of light transmission by dense canopy or because of logging disturbance. For this reason and because PC1 explained the majority of the variation, I did not pursue separate analyses with PC2 despite the two principal components being uncorrelated.

Carbon flow from resources to predators

Irrespective of habitat complexity, leaf litter had less isotopic variation than fresh leaves (LME, Resource, $F_{1, 22} = 7.645$, $P = 0.011$), but the isotopic variation of the two resource types responded similarly to the PC1 gradient (LME, PC1 x Resource, $F_{1,22} = 0.494$, $P = 0.489$). However, the isotopic variation in basal resources responded differently to habitat degradation among years (LME, PC1 x Year, $F_{2,22} = 3.682$, $P = 0.042$; Figs. 4.3D and E). In 2015 isotopic variation increased along PC1, with the inverse in 2016 and 2017. The variation in these resources differed among years (LME, Year, $F_{2,22} = 4.826$, $P = 0. 018$), although pairwise comparisons showed no significant differences between any combination of years ($Pc > 0.05$; Fig. 4.5B).

Mean $\delta^{13}C$ measured on wing tissue of bat assemblages increased across PC1 (LME, PC1, $F_{1,62} = 30.186$, $P < 0.001$; Fig. 4.3A). The response across PC1 differed between years (LME, PC1 x Year, $F_{2,62} = 14.588$, $P < 0.001$), with the largest increase in 2016, and much weaker relationships in 2015 and 2017. Mean $\delta^{13}C$ differed among bat species (LME, Species, $F_{7,62} = 11.722$, $P < 0.001$) and years (LME, Year, $F_{2,62} = 96.7405$, $P < 0.001$).

Trophic position of predator populations

The impact of habitat degradation (PC1) on trophic position of bat populations differed between years (LME, PC1 x Year, $F_{2,53}$ = 53.251, P <0.001; Fig. 4.3B), with a strong negative relationship in 2015 and a weak positive relationship in the subsequent two years. The response of trophic position to canopy height closely followed the response over PC1, albeit the inverse as primary forest was associated with the highest values of canopy height (LME, CH x Year, $F_{2,57}$ = 45.789, P <0.001; supplementary Fig. S4.3A). Mean trophic position differed among species (LME, Species, $F_{7,56}$ = 4.409, P <0.001) and years (LME, Year, $F_{2,57}$ = 56.032, P <0.001), higher in 2015 compared to subsequent years (P_c (2016- 15) = 0.039; (2017- 15) = 0.001).

Isotopic diversity of predators and their prey

When investigating the response of trophic range (range $\delta^{15}N$) for bat communities, PC1 was not retained in the model, and the relationship among years was non-significant (LME, $F^{2,10}$ = 2.648, P = 0.119). Neither was the variation in carbon resources (range $\delta^{13}C$) explained by PC1 (LME, $F_{1,6}$ = 0.977, P = 0.362), and sample year was not retained in the best model. Similarly, at the population level neither PC1 or forest cover were retained in the best model of bat multivariate isotopic niche breadth (supplementary Fig. S4.3B). Furthermore, there were no among-year differences in the multivariate isotopic variation for bat populations (LME, $F_{2,72}$ = 1.788, P = 0.175). There was also no relationship between the isotopic variations of three insect trophic groups (carnivores, detritivores and herbivores) and the PC1 axis (2017 data only; LME, $F_{2,11}$ = 0.098, P = 0.907).

Trophic redundancy of predator communities

The impact of habitat disturbance, represented by PC1, on mean nearest neighbour distance in isotopic niche space (MNND) differed among years (LME, PC1 x Year, $F_{2,12}$,

$P = 0.041$; Fig. 4.3C). In 2017 there was a very strong indication of decreased resilience at sites with lower forest complexity, with a 67% increase in MNND from primary to repeatedly logged secondary forest (based on the slope of the line in Fig. 4.3C). However, in 2015 and 2016 there was no clear relationship. Furthermore, this metric differed among years, irrespective of site identity (LME, Year, $F_{2,12}$, $P = 0.011$), although pairwise comparisons showed no differences between any combination of years ($Pc > 0.05$; Fig. 4.5A). There was also no difference across the gradient of habitat disturbance or among years for standard deviation of nearest neighbour distance (SDNND; LME, $F_{1,5} = 0.002$, $P = 0.967$).

Tables and Figures

Table 4.1. Resultant values for the first four axes of the Principal Component Analysis, based on vegetation metrics (n=21), showing the values along each PC axis (1-4).

Site	PC1	PC2	PC3	PC4
D	4.135	1.154	0.114	-0.209
C	3.820	0.917	-0.071	-0.233
E	3.720	0.689	-1.324	0.149
F	0.652	-0.934	0.476	0.297
B	-0.146	-1.877	1.354	-1.196
LFE	-1.338	-2.668	-1.025	0.875
DVCA	-3.340	1.521	1.636	1.054
MBCA	-7.503	1.199	-1.160	-0.736

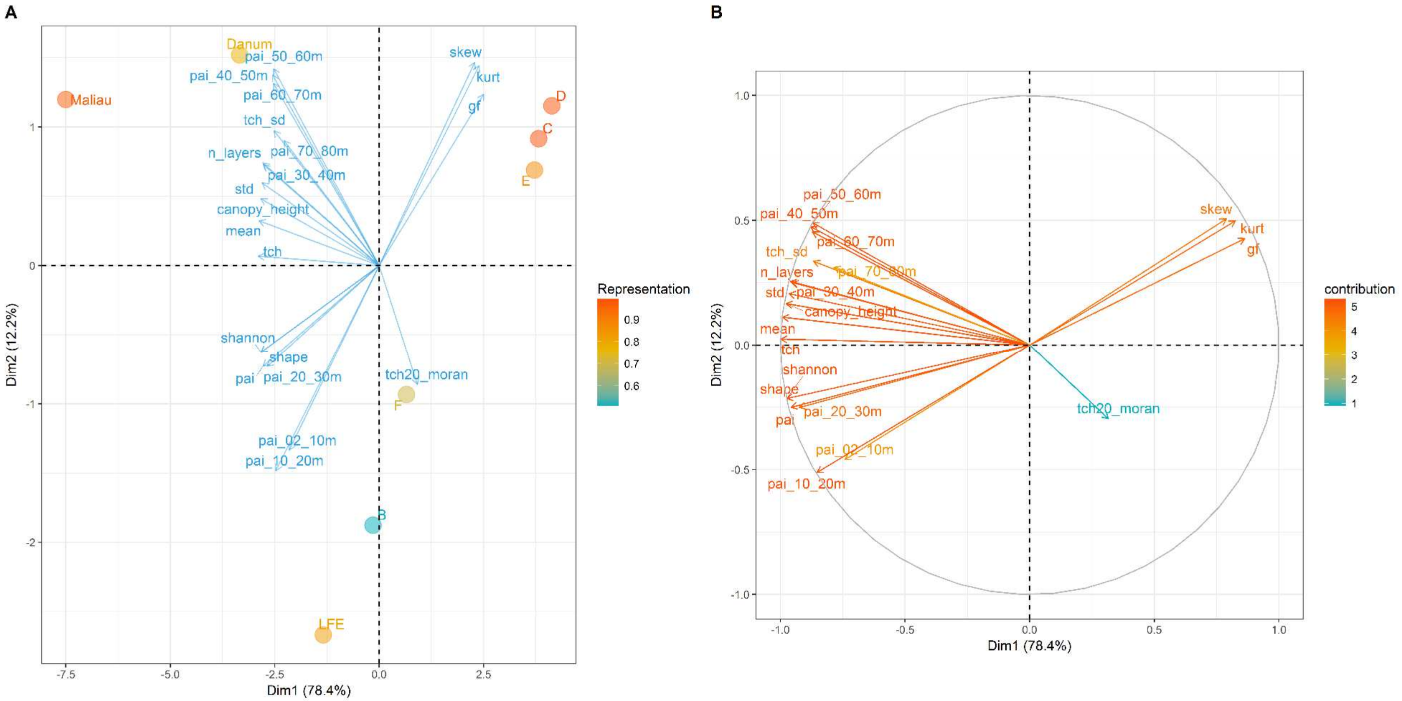


Figure 4.1. [A] Vegetation structure of sample sites grouped by similarity of their vegetation structure. A gradient bar illustrates the quality of site representation, with red indicating good representation, and blue indicating poor representation. Blue arrows represent vegetation metrics (n= 21) extracted from LiDAR data. Positively correlated variables point to the same side of the graph and negative correlated variables point to opposite sides. [B] Represents only LiDAR metrics and here the gradient indicates how variables contribute to the principal components, where red indicates high contributions, and blue indicates low. PC1 explains 78.4 % of the variation between sites, and PC2 explains a further 12.2 % of the variation. The derived PC1 axis represents an intuitive ecological gradient of vertical structural complexity from primary forest to repeatedly logged forest.

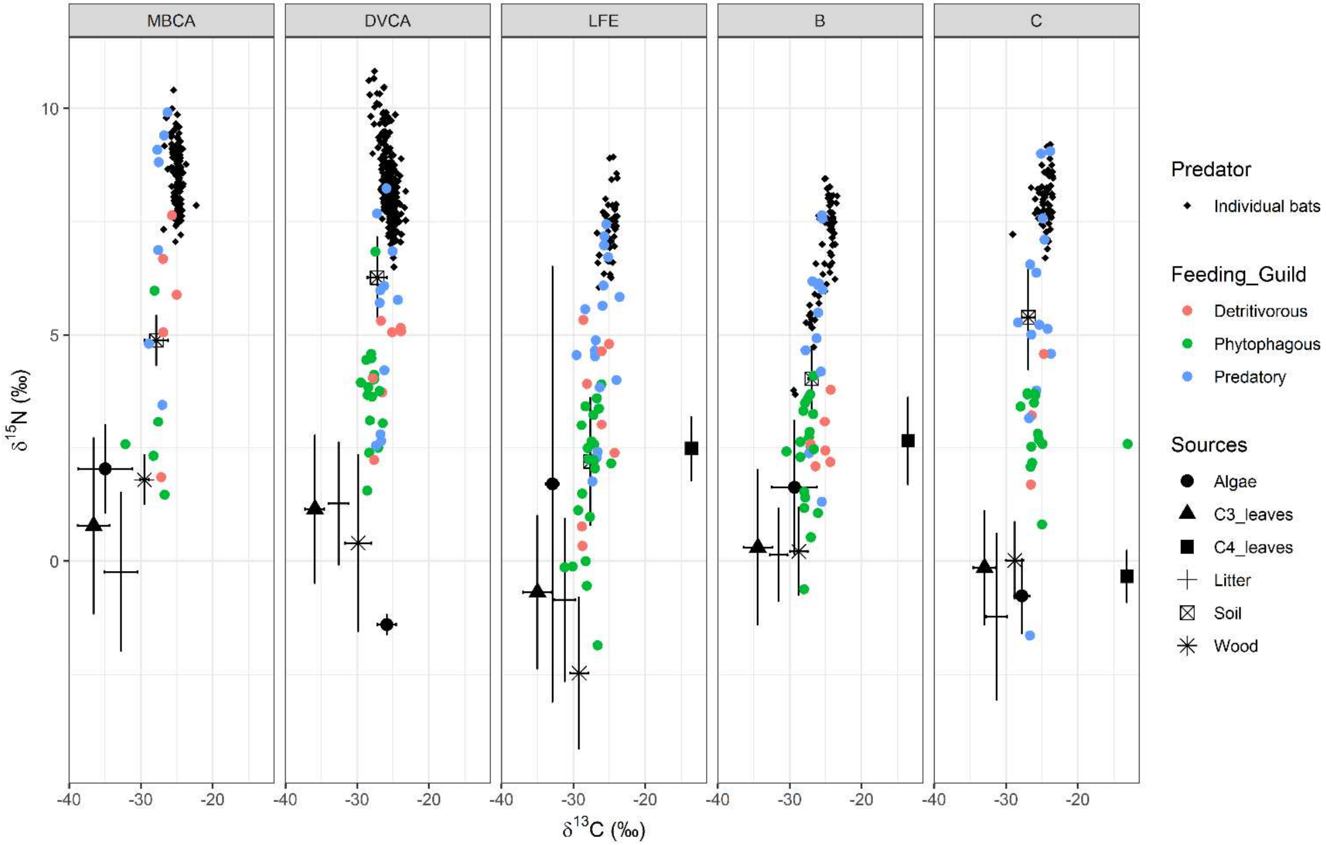


Figure 4.2. Bi-plot representing C and N composition of bat predators, insect prey and basal resources where black diamonds represent bat individuals, coloured circles illustrate the isotopic values of different insect guilds (red = detritivore, green = herbivore, and blue = carnivore). Large black shapes represent the different basal resources. Error bars represent SD around the mean values for source populations. Bats and insect values are not baseline corrected, and therefore their absolute nitrogen values are not comparable across sites.

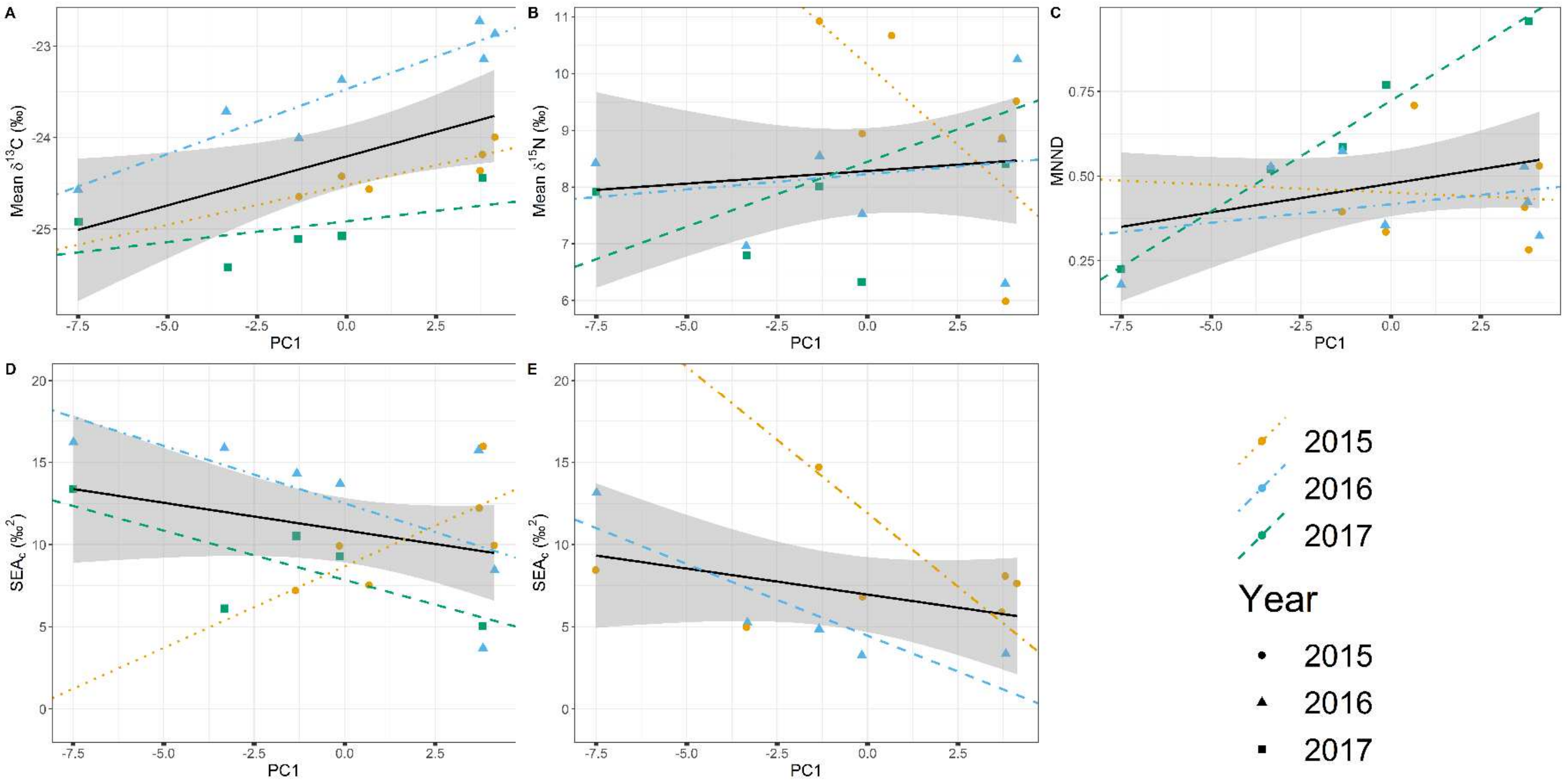


Figure 4.3. Relationships between vegetation structure metrics, represented by principal component axis 1 (PC1; Fig.4.1; where more negative PC1 values indicate higher quality forest), and [A] mean $\delta^{13}C$ and [B] mean trophic position and [C] trophic redundancy of bat communities. Panels [D] and [E] represent the relationship between PC1 and isotopic variation (SEAc; ‰^{2}) of leaves and leaf litter, respectively. The symbols show food web metrics calculated at each site for three different years (circle = 2015; triangle = 2016, and square = 2017). The solid line is the global relationship and the shaded area is ± 1 standard error. The additional lines represent the modelled relationship for each year (orange line is 2015; blue line is 2016, and green line is 2017).

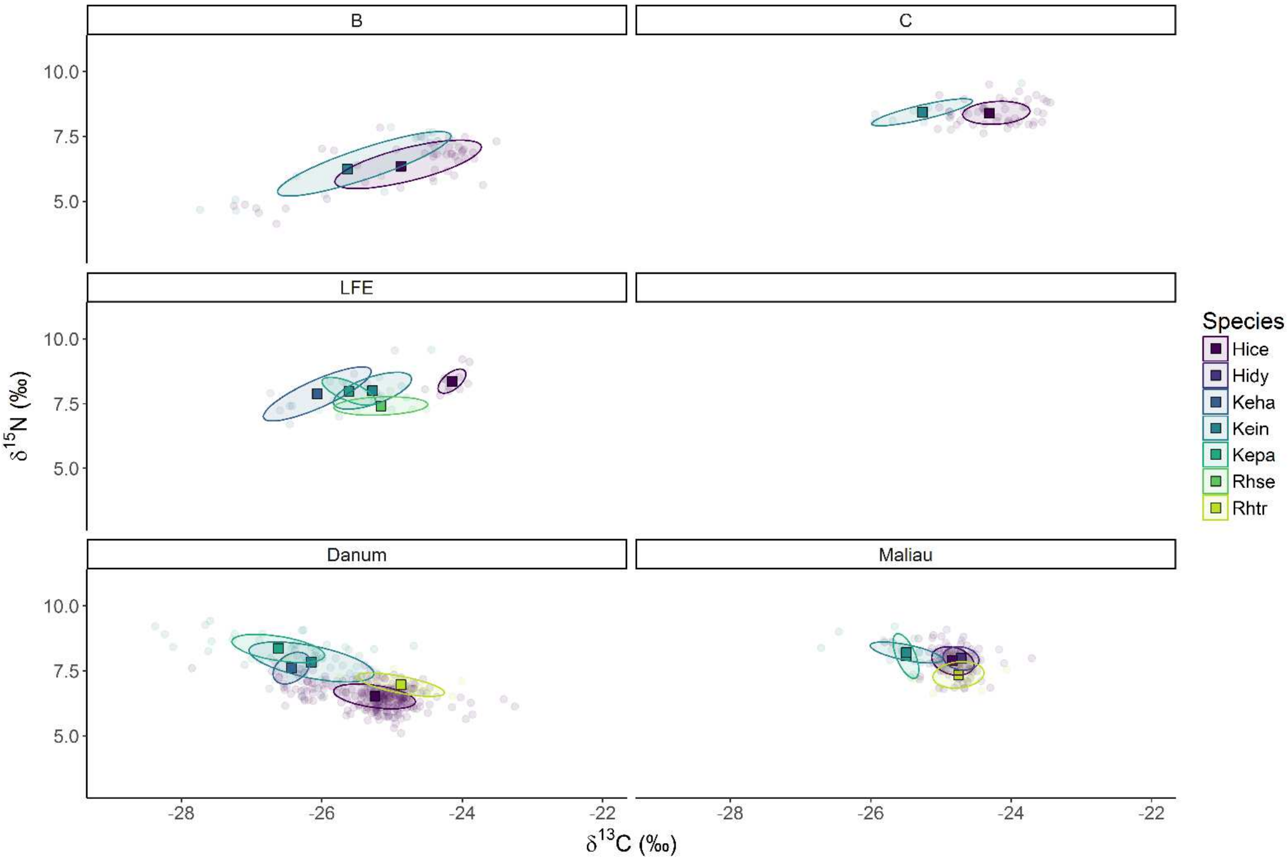


Figure 4.4. Isotopic niches of bat populations across the five sites sampled in 2017. Sites are separated into rows by habitat type (top = disturbed secondary forest, middle = intact secondary forest, and bottom = primary forest). Bat populations include five or more conspecific individuals captured at harp trap locations within a sampled site, and isotopic niches represent 40 % of the isotopic variation for a given population. Isotopic values for individual bats is plotted as faint circles, and squares represent the population centroids, which underlie the calculation of mean nearest neighbour distance (MNND).

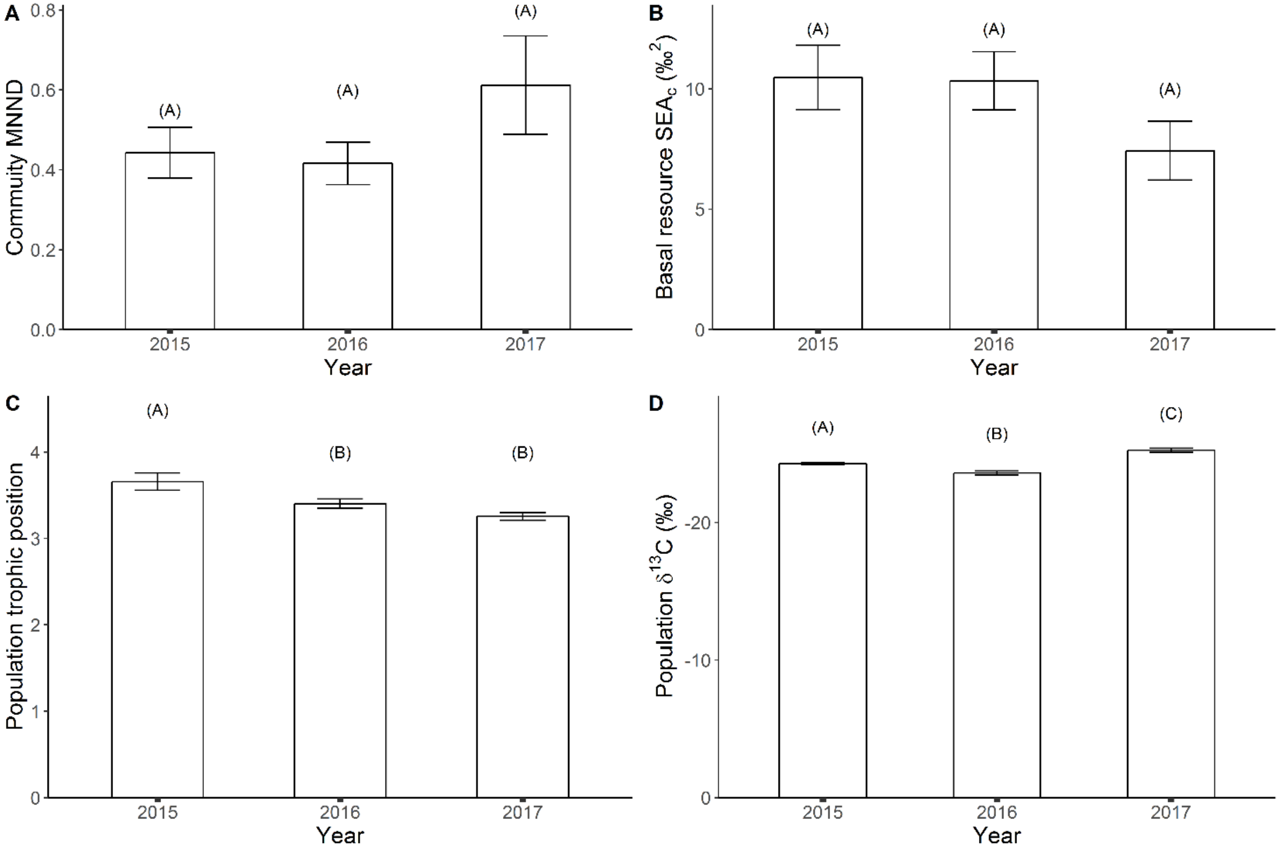


Figure 4.5. Year-specific mean ± SE [A] mean nearest neighbour distance (MNND) calculated for bat communities, [B] standard ellipse area, adjusted for sample sizes (SEAc, ‰) of basal resources (fresh leaves and leaf litter), and [C] trophic position and [D] δ^{13}C calculated for bat populations. Metrics plotted are those for which the fixed term year was retained in the best model, and was significant (AIC comparison of candidate models; supplementary Tables S4.11-S4.13). Letters above bars denote whether year-specific means were significantly different from one another, with Bonferroni correction for multiple tests.

Discussion

Carbon stable isotope ratio ($\delta^{13}C$) measured on wing tissue of abundant bat species became increased with forest degradation, potentially implying that bat assemblages altered their resources use across the spatial gradient of habitat complexity. Interannual changes in bat $\delta^{13}C$, likely linked to drought stress, were of a similar magnitude to changes occurring with the long-term effects of logging, and caused shifts in the same direction. If interannual effects are driven by drought, future climatic events may alter the resource use of tropical bat communities in similar ways to the impacts of logging. The synergistic effects, especially over longer-term climatic changes could severely alter and destabilise food web structure. Furthermore, predator trophic position and resilience-related metrics, and isotopic variance of basal resources differed among years in their relationship with forest degradation, indicating potentially short-term impacts on food web structure and dynamics.

LiDAR data captured the long-term effects of previous logging upon vegetation structure at sample sites, and should be well related to the long-term effects upon bat communities. The derived PC1 axis provided an intuitive ecological gradient from primary forest to repeatedly logged forest. Given that all variables contribute substantially to PC1, albeit a weaker contribution from Moran's I for top-of-canopy height, the axis provides a useful description of forest structural complexity. Research sites did not differ in horizontal variation in top-of-canopy height, estimated by Moran's I, despite previous evidence of reduction in regenerating forest (Okuda *et al.* 2003). This suggests similar rates of gap formation, and thereby age uniformity of canopy-forming trees across our sites with different habitat disturbance. Indeed, treefall gaps are considered a common part of healthy forest dynamics (Edwards *et al.* 2014a). However, horizontal structure can be context dependent, whereas canopy height is consistently lower in degraded compared to natural habitats (Rutten *et al.* 2015). I interpret all interannual changes in the context of regional climatic changes driven by El Niño, as well as active disturbance across the SAFE landscape. Any interannual changes in mean response, irrespective of habitat, likely indicate very short-term affects (1-2 years) of drought stress upon bat diet, given that drought conditions lead to pronounced defoliation (David Coomes, personal communication) and negatively affect forest ecosystems (Anderegg *et al.* 2015).

Predator resource use over space and time

Bat (mean) $\delta^{13}C$ was the only variable that changed across the gradient of habitat complexity, having increased in less complex forest, potentially indicating a shift to reliance upon more ^{13}C-enriched prey. The ^{13}C-enrichment at repeatedly logged sites compared to primary forests is approximately 2‰, which is in the range of indicating divergent foraging strategies (Sullivan *et al.* 2006). Bat $\delta^{13}C$ values also varied among years, irrespective of habitat, suggesting that all sites were commonly experiencing some environmental pressure. The interannual differences in the relationship between $\delta^{13}C$ and habitat complexity also suggests that the impact of that environmental pressure may be habitat-dependent. There was an overall ^{13}C-enrichment of wing tissue in 2016 and then more pronounced shift in the opposite direction in 2017, depleting to below 2015 levels. This might indicate that between years, bat populations were temporarily shifting their dependence upon different resource types. The changes in $\delta^{13}C$ between years are of a similar magnitude to that occurring with habitat simplification, approximately 1 and 2‰, respectively. El Niño is known to cause similar structural changes to logging impacts, *i.e.* shorter canopy with drought-induced defoliation (David Coomes, personal communication), implying that $\delta^{13}C$ shifts could have similar underlying mechanisms.

Given our expectation of reduced litter inputs in regenerating forest (Villela *et al.* 2006), I hypothesized a shift towards green energy channels, *i.e.* ^{13}C-depletion of wing tissue. Our finding of ^{13}C-enrichment with habitat simplification could suggest an increased dependence on leaf litter, or woody material, both ^{13}C-enriched compared to living C_3 leaves. Indeed, the relatively small magnitude of the shifts are as expected, given the narrow separation between brown and green resources in this tropical forest ecosystem (Table S10; Fig. 4.2), compared to resources with more dispersed carbon values, along a lake depth gradient (Vander Zanden & Rasmussen 1999) or between freshwater and marine (Fry & Sherr 1984) for examples. High density of woody debris in post-logging forest could result from small logs of no commercial value discarded during the logging process as well as from trees which died several years after harvesting (Blanc *et al.* 2009), especially given high biomass accumulation rates in regenerating forests (Berry *et al.* 2010). Despite shifts in predators' resource use, there was no change in isotopic variation of basal resources across the gradient of habitat complexity. However, leaf litter is composed of multiple plant species which differ in decomposability (Prescott 2002), and therefore collected samples may under- or over-estimate available inputs to the detrital web among sites with different canopy species compositions (Denslow 1987; Villela et al. 2006).

The aforementioned counter-shifts between years, as well as consistency among habitats, *i.e.* not localised to areas of active disturbance, suggests that the observed interannual shifts may reflect impacts of El Niño intensification, and subsequent abatement. I postulate that changes in predator resource use reflected drought-induced alterations to the community composition of insect guilds across our suite of sites. I found no changes in C:N ratio of C_3 understorey leaves among years or across the gradient of habitat complexity (LME, $F_{1,5} = 0.362$, $P = 0.573$; Fig S4.5), indicating that understorey plants did not reduce nutritional content during drought period (Domingues *et al.* 2018). However, drought can cause shifts to insect community composition due to abiotic interference with development rates and aspects of species' demography that drive abundance at emergence and population success (Anderegg *et al.* 2015). Given that the shift in $\delta^{13}C$ during drought intensification was additive to the shift with degradation, secondary forest is more likely to experience extreme shifts, which may decrease the structural asymmetry of food webs and decrease resilience to future perturbations (McCann *et al.* 2005).This would raise the question of whether local bats changed their diet and/or foraging behaviour in response to altered prey resources, or bat individuals with altered levels of specializations that match food abundance in disturbed habitats settled in these specific areas.

Observed shifts in predator $\delta^{13}C$ values among years could also reflect shifts in resources use by predators, not associated with the composition of prey guilds in the diet, but rather the primary resources upon which the herbivorous insects are primarily feeding. For examples, ^{13}C-enrichment of wing tissue of the magnitude observed could reflect a shift from a C_3 to a C_3/C_4 base (Sullivan *et al.* 2006), or from understory to canopy trees (Crowley *et al.* 2013). Furthermore, shifts in predator $\delta^{13}C$ values could also reflect changes associated with their diet, but more subtle than shifts from one resource type to another. Previous studies have found differences in $\Delta\delta^{13}C$ between resource and consumer depending on the relative proportion of animal and plant material in the diet (McMahon *et al.* 2010), and nutritional status of the consumers (Gorokhova 2017). The former is unlikely as insectivorous bat communities do not subsidise their diet with plant material, as is the case in Paleotropic assemblages (Rex *et al.* 2010). Seltmann *et al.* (2017) found a weak relationship between capture location and body mass, and no interannual change in body mass for bat populations across our study area, suggesting that the diminished nutritional status found to reduce $\Delta\delta^{13}C$ in other taxa (Gorokhova 2017) is unlikely to underlie our results. Lastly, the effects of drought on C_3 plant physiology could cause ^{13}C-enrichment of leaves (Jucker *et al.* 2017), which would be reflected in the isotopic values of consumers throughout the length of the food chain (Fry 2008).

Contrary to expectation, there was no general relationship between trophic positions of bat populations and habitat complexity. However, in 2015 there was a strong relationship between trophic position and both structural complexity (Fig. S4.3B), and canopy height as a single predictor (supplementary Fig. S4.3A). This relationship was absent in subsequent years when I included primary forest sites in the gradient of habitat complexity. The disparity in patterns between years could be explained by context-dependence of the importance of the two major drivers of food chain length: productivity and ecosystem size (Post 2002a; Takimoto & Post 2013; Ward & McCann 2017). The strong relationship when considering only secondary forest could be due to reduced ecosystem size at all SAFE sites compared to LFE, which remains contiguous with Ulu Segama reserve. If all secondary forest sites are in the phase of low productivity (Berry *et al.* 2010), I would expect the increased ecosystem size of LFE to support longer food chains compared to other secondary sites (Ward & McCann 2017). On the other hand, our large and productive primary forest sites may be associated with shorter food chains due to a higher prevalence of omnivory (Ward & McCann 2017). That said, a subset of our regenerating forest fragments do not appear to differ in net primary plant productivity compared to old-growth forest (Riutta *et al.* 2018), but they may differ in other characteristics which interact with productivity.

There were among-year differences in mean trophic position irrespective of habitat type. Trophic position was lower in 2016 and 2017 compared to 2015, indicating short-term response to an emergent pressure. This could be a response to El Niño, whereby dynamic constraints prevent long food chains establishing under severe disturbance (Takimoto & Post 2013). Although the magnitude of the change in trophic positions is very low, even small changes in nitrogen stable isotope ratios could result in considerable changes to trophic dynamics (Post 2002b), including degree of intra-guild predation. Alternatively, reductions in trophic position across the three years of study could reflect decreased nutritional status of the populations due to drought stress upon the forest and associated insect communities. The same trophic enrichment factor ($\Delta\ \delta^{15}N$) is used to calculate trophic position for all three years, which may be an over-estimate for individuals of impaired nutritional status (Gorokhova 2017).

Isotopic diversity of upper trophic levels over space and time

Neither among years nor across the gradient of habitat complexity was there any reduction of isotopic variation for bat populations or their insect prey, in general or for detritivores, herbivores or carnivores separately. Isotopic variation for species and functional groups summarises dietary information (Newsome *et al.* 2007). Although habitat degradation can be associated with reduced niches, following simplification of food chains and reduction in available resources (Layman *et al.* 2007b), there is also evidence for niche expansion due to abiotic forcing of reduced dietary discrimination toward preferred resources (Reddin *et al.* 2016). The lack of relationship between isotopic variation and habitat characteristics could also reflect that the latter do not affect the diversity of insect prey available to bats. The midstorey and understorey habitat structure may have been under-represented in our method of habitat characterisation compared to their relevance to bat foraging. Below-canopy structure is strongly correlated with insect community composition (Kitching *et al.* 2013) and bat habitat use (Dodd *et al.* 2012; Müller *et al.* 2013). Additional predictors of bat habitat use and the trait-environment relationship more suitable then canopy cover may include components of the understorey cover below 20m of height (Blakey *et al.* 2017). Although these metrics are not available for our sites, they may have a direct relevance to the among-site differences in isotopic variation of insect prey and bat predators.

Trophic redundancy and other food web metrics

Mean nearest neighbour distance (MNND) of bat assemblages varied among years, with a strong but non-significant increase (indicating reduced trophic redundancy) in 2017 compared to preceding years (Fig. 4.3C). The altered relationship between trophic redundancy and habitat complexity is driven by the strong increase in MNND with habitat simplification in 2017. The increased separation between population centroids at lower quality sites (Fig. 4.4) appears to be principally driven by differences in $\delta^{13}C$. But, the strong relationship in 2017 could be influenced by low number of species considered in the disturbed secondary sites (Layman *et al.* 2007a). Differential responses of bat functional groups, *i.e.* separating by call type or forging range, to altered resource availability in the disturbed SAFE landscape could induce niche separation along the carbon axis. Although I have not investigated inter-guild responses to habitat degradation in this study, terrestrial predators have exhibited guild-specific flexible foraging strategies with impacts on their carbon stable isotope ratios (Perkins *et al.* 2018).

Capture of spatial and temporal environmental changes

Observed interannual differences in the relationship between food web response and habitat complexity could indicate habitat-specific response to regional climatic stress. Among-year differences in the relationship of the response across our gradient of habitat complexity could also reflect alteration to dynamics at the SAFE sites due to modification of the forest within the foraging range of some bat species. The habitat fragmentation can influence insect community and bat habitat use (Kricher 2011) through edge effects, and changes to abiotic factors such as temperature and humidity (Kupfer *et al.* 2006). Unfortunately there are no data on active logging at the SAFE, nor the impact of drought on different habitat types. Finally, some year-specific responses could also be driven by the effect of site inclusion, such as the absence of primary forest sites in 2015.

I optimised habitat assessment to the average foraging range of insectivorous bat communities, but these in reality consist of guilds with differing ecology. Due to guild-specific importance of landscape characteristics at different spatial scales (Ducci *et al.* 2015), it would be interesting to test the effects of habitat degradation upon bat communities at a range of relevant scales. I opted for a maximum buffer area of 1 km in order to limit the extent to which extreme values at local scales are moderated towards the landscape mean. However, our habitat metrics may be less relevant to the scale at which very narrow-foraging species (< 200 m) or wide-ranging species (up to 2 km) perceive disturbance effects. For wider-ranging species, this may be particularly pertinent in a degraded environment. During periods of reduced prey density, aerial hawking bats exploit more distant foraging patches to avoid exploitation competition by aggregations of heterospecifics, *i.e.* for food items and flight space (Roeleke *et al.* 2018). Thus, diet composition of bat assemblages could be influenced by habitat degradation at much larger spatial scales than measured here.

Conclusions

Predator trophic position, resilience-related metrics for predator communities and isotopic variance in basal resources differed among years, and in their relationship with forest degradation. Moreover, predator resource use shifted with long-term reduction in habitat complexity, and in response to short-term pressures, towards more ^{13}C-enriched resources. If climatic conditions indeed drive the observed interannual effects, climate change may influence tropical bat communities in a similar manner, and by comparable magnitude, to the impacts of forest degradation and conversion. Although the magnitude of effects upon community resource use are relatively small, they may increase under the synergistic effects of forest degradation and climate change. Forest clearing can disrupt climate regulation, increase environmental temperature and intensify El Niño events, themselves associated with unusually hot and dry conditions compared to the long-term average (McAlpine *et al.* 2018). Understanding the interactive effect of climate and local stressors is a major challenge for mitigating complex biotic responses (Barlow *et al.* 2018). Our study thus indicates potentially increased severity of changes to food web structure and ecosystem function under the future additive impacts of forest degradation, habitat simplification, and climate change. This is particularly poignant in South East Asia, where large areas of logged forest and agriculture will be major features of future tropical forest landscapes.

Supplementary Methodology (Chapter 4)

S4.1. Quality control of bat wing tissue delta values

Avoiding heavily preganant, recently recaptured, juvenille and distressed bats I collected wing punches from 2617 individuals. After accounting for samples which were lost during laboraory processing or for which I were unable to match field and laboratory records, I returned 2213 isotopic values for individual bats. Furthermore, I excluded values which had insufficient elemental content to provide an accurate delta value. Based upon the fact that nitrogen delta values are more sensitive to low elemental content than carbon delta values, I excluded samples which had a nitrogen beam area below 1.30e-08, which excluded a further 17 observations, and gave a total 2196 individual isotopic values. By year this provided 529 samples in 2015; 879 in 2016 and 788 in 2017.

S4.2. Accuracy of isotopic measurements

In order to assess accuracy of isotopic measurements on bat wing tissue, and leaf, litter and insect material, I calculated the mean and standard deviation of isotopic measurements on casein IRMS standard.

Material	caesin mean	caesin SD	n
Wing tissue 2015	5.909	0.352	114
Wing tissue 2016	5.942	0.147	125
Wing tissue 2017	5.878	0.614	110
C3 leaves 2015	5.975	0.708	14
C3 leaves 2016	6.195	0.571	17
C3 leaves 2017	6.003	0.128	20
Litter 2016	6.044	0.306	18
Litter 2017	6.058	0.351	21
Insects 2017	5.917	0.223	22

Supplementary Tables (Chapter 4)

Tables S4.1. Number of individuals included in the species-specific means at each site for the three sample years. These number reflect individuals which were captured, fit for taking a wing punch, and for which samples were retained after quality control for analytical error. Values in grey reflect sites not sampled in a given year. Emboldened values are where numbers are >= 5; below which populations were excluded from SIBER.

Sample Site	Habitat Type	Species	2015	2016	2017
B	Repeatedly logged	Hice	**18**	**22**	**45**
		Hidy	0	1	2
		Keha	**23**	3	2
		Kein	**26**	**20**	**16**
		Kepa	2	4	0
		Rhbo	1	2	1
		Rhse	**5**	**5**	3
		Rhtr	**10**	**12**	4
C	Repeatedly logged	Hice	**33**	**42**	**50**
		Hidy	1	0	0
		Keha	**23**	4	2
		Kein	**28**	**12**	8
		Rhbo	**5**	1	2
		Rhse	4	1	4
		Rhtr	**10**	2	3
D	Repeatedly logged	Hice	0	4	0
		Hidy	**13**	**6**	0
		Keha	**13**	**14**	0
		Kein	**18**	**14**	0
		Kepa	1	2	0
		Rhbo	0	1	0
		Rhtr	**10**	2	0
E		Hice	**6**	**8**	0
		Hidy	1	**8**	0
		Keha	**19**	**8**	0
		Kein	**21**	**13**	0
		Kepa	2	3	0
		Rhbo	1	1	0
		Rhse	**6**	**13**	0

		Rhtr	**6**	**5**	0
F	Repeatedly logged	Hice	5	0	0
		Hidy	**14**	0	0
		Keha	**8**	0	0
		Kein	**15**	0	0
		Kepa	2	0	0
		Rhbo	3	0	0
		Rhtr	3	0	0
LFE	Twice-logged	Hice	**5**	**14**	**11**
		Hidy	4	2	**9**
		Keha	**9**	2	**6**
		Kein	**22**	**12**	**12**
		Kepa	**12**	3	**5**
		Rhbo	3	0	3
		Rhse	**5**	**7**	5
		Rhtr	**5**	**7**	4
MBCA	Primary	Hice	0	**73**	**73**
		Hidy	0	**15**	**23**
		Keha	0	3	3
		Kein	0	**24**	**17**
		Kepa	0	**11**	**5**
		Rhbo	0	**44**	**22**
		Rhse	0	**5**	1
		Rhtr	0	**14**	**12**
DVCA	Primary	Hice	0	**108**	**267**
		Hidy	0	0	1
		Keha	0	**10**	**7**
		Kein	0	**36**	**45**
		Kepa	0	**24**	**12**
		Rhbo	0	1	3
		Rhse	0	**10**	4
		Rhtr	0	**9**	**15**

Table S4.2. Broad taxonomic composition of insects included in guilds' ellipse-based metrics (SEAc, ‰^{2}) for isotopic variation. Feeding guilds are assigned based on larval feeding, and taxomomic annotation was made to family and sub-family level where required to ascertain feeding guild.

Feeding guild	**Order**	**MBCA**	**DVCA**	**LFE**	**B**	**C**
Detritivore	Blattodea	2	2	0	2	0
	Coleoptera	3	5	7	3	0
	Diptera	0	0	1	1	0
Herbivore	Coleoptera	3	8	13	11	10
	Diptera	0	0	1	0	0
	Hemiptera	0	6	7	7	3
	Hymenoptera	2	0	1	0	1
	Lepidoptera	0	2	1	1	0
Predator	Araneae	0	0	1	0	0
	Coleoptera	1	5	2	4	4
	Diptera	0	0	0	1	0
	Hemiptera	0	0	3	0	0
	Hymemoptera	0	0	0	4	0
	Hymenoptera	6	6	12	4	10
	Psocoptera	0	1	0	0	0

Tables S4.3. Samples of basal resources (representing major inputs to green and brown food web compartments) included in resource-specific ellipse-based metrics (SEAc, ‰^{2}) for isotopic variation.

Site	C_3 Leaves			Leaf litter		
	2015	2016	2017	2015	2016	2017
MBCA	-	20	19	-	27	10
DVCA	-	10	30	-	11	30
LFE	7	20	20	-	19	19
B	14	17	19	-	16	20
C	6	10	18	-	10	18
D	17	8	-	-	9	-
E	18	19	-	-	20	-
F	8	-	-	-	-	-

Table S4.4. LiDAR index metrics of vegetation structure and habitat complexity. Metrics were extracted from LiDAR point clouds collected over SAFE, Maliau and Danum in September and October 2014. Set 1 were extracted from the 50 cm resolution canopy height model raster – except for Moran's I, which was calculated after aggregating the canopy height model raster to 20 m resolution. Set 2 were extracted from vertical plant area density profiles at 20 m resolution – except for Canopy height which was extracted directly from the canopy height model point cloud.

Metric	Code	Unit	Definition
Set 1			
Top-of-canopy height	tch	m	Average of top canopy height
Top-of-canopy height standard deviation	tch_sd	m	Standard deviation of the canopy height model raster
Gap fraction	gf	proportion	The proportion of the canopy area lower than 10 m in height
Moran's I	tch20_moran		Describes canopy height aggregation in horizontal space. Range -1 to 1: -1 indicates perfect dispersion; 0 indicates random distribution; and 1 indicates perfect clumping. In practical terms, values closer to 1 indicate the presence of different habitat types, which are clumped in space.
Set 2			
Canopy height	canopy height	m	The 99th percentile of the point cloud vertical profile; *i.e.* the maximum canopy height
Mean	mean		The centroid of the plant area density profile
Kurtosis	kurt		Higher values indicate canopies that are strong clustered around the mean.
Number of layers	n_layers		Number of *contiguous* canopy layers with a PAD greater than a user-defined threshold (0.1 I think initially)
Plant area density	PAI	$m\ m^{-2}$	The plant area index. Equivalent to Leaf area index but includes stems

Plant area density 2-10 m	pai_02_10m	m m^{-2}	The plant area index of slices through the vertical canopy profile.
Plant area density 10-20 m	pai_10_20m		
Plant area density 20-30 m	pai_20_30m		
Plant area density 30-40 m	pai_30_40m		
Plant area density 40-50 m	pai_40_50m		
Plant area density 50-60 m	pai_50_60m		
Plant area density 60-70 m	pai_60_70m		
Plant area density 70-80 m	pai_70_80m		
Shannon index	Shannon		The diversity of vertical plant area index profile; *i.e.* the diversity of niches available.
Shape	Shape		Ratio of maximum plant area index and 99th percentile of point cloud vertical profile; the position of maximum canopy density as a proportion of maximum canopy height.
Skew	Skew		Negative values indicate more leaves in the lower profile; positive values indicate more leaves in the upper profile.
Std	Std		The standard deviation of the plant area density profile.

Table S4.5. Vegetation structure characteristics of the sampling sites representing the three different habitat types, primary forest, intact secondary forest and disturbed secondary forest. Site-specific estimates are averaged across a polygon representing a 1 km buffer around the mean coordinates of all successful harp traps locations at that site, weighted by the number of captures across all three years.

Site	Habitat Type	Top-of-canopy height (m)	Top-of-canopy height SD (m)	Gap fraction (%)	Top-of-canopy height Moran's I (-1 to 1)	Canopy height (m)	Kurtosis	Shannon	Skew	Shape
MBCA	Primary	35.2	12.51	0.04	0.58	52.48	3.1	3.33	0.76	3.33
DVCA	Primary	26.16	13.48	0.13	0.52	45.67	5	2.88	1.31	2.88
LFE	Twide-logged	21.04	8.23	0.12	0.71	31.08	3.64	2.9	0.87	2.9
B	Repeatedly logged	17.31	6.38	0.12	0.51	28.1	3.91	2.77	0.98	2.77
C	Repeatedly logged	9.25	6	0.61	0.61	19.79	6.05	2.21	1.46	2.21
D	Repeatedly logged	8.99	5.86	0.6	0.6	18.68	6.28	2.14	1.54	2.14
E	Repeatedly logged	9.39	6.82	0.61	0.68	20.04	5.39	2.26	1.35	2.26
F	Repeatedly logged	17.36	7.87	0.18	0.61	28.89	4.72	2.67	1.25	2.67

Site	Habitat Type	Mean (centroid of PAD)	Number of layers	PAD	SD (of PAD)	PAD 2-10m	PAD 10-20m	PAD 20-30m	PAD 30-40m	PAD 40-50m	PAD 50-60m	PAD 60-70m
MBCA	Primary	18.36	4.15	7.74	13.28	2.55	1.82	1.18	0.77	0.54	0.29	0.05
DVCA	Primary	14.06	3.46	6.38	11.82	2.8	1.29	0.61	0.43	0.36	0.19	0.03
LFE	Twice-logged	11.1	2.23	6.43	7.57	2.71	1.79	0.97	0.24	0.02	0	0
B	Repeatedly logged	9.27	1.76	5.66	6.46	2.78	1.59	0.43	0.06	0.01	0	0
C	Repeatedly logged	6.29	1.38	3.2	4.54	1.76	0.6	0.12	0.01	0	0	0
D	Repeatedly logged	5.98	1.35	3.07	4.35	1.73	0.52	0.1	0.01	0	0	0
E	Repeatedly logged	6.73	1.37	2.69	4.83	1.35	0.62	0.13	0.02	0.01	0	0
F	Repeatedly logged	8.87	1.84	5.09	6.79	2.52	1.15	0.44	0.11	0.02	0	0

Table S4.6. Isotopic variance as standard ellipse area (SEAc, ‰^{2}) for basal resources at all 8 sites across three sample years, calculated when be obtained >= 5 samples at a given site.

Site	SEAc leaves			SEAc litter		
	2015	2016	2017	2015	2016	2017
MBCA	-	16.234	13.381	-	8.447	13.157
DVCA	-	15.871	6.120	-	4.963	5.249
LFE	7.210	14.329	10.520	-	14.703	4.863
B	9.917	13.706	9.305	-	6.820	3.262
C	15.976	3.697	5.025	-	8.086	3.353
D	9.942	8.432	-	-	7.637	-
E	12.222	15.752	-	-	5.891	-
F	7.535	-	-	-	-	-

Table S4.7. Isotopic variance as standard ellipse area (SEAc, ‰^{2}) for insect guilds at six sites in 2017, calculated when be obtained >= 5 samples at a given site.

Site	SEAc phytophage	SEAc detritivore	SEAc predator
MBCA	6.916	15.198	7.254
DVCA	3.030	5.117	7.315
LFE	11.923	9.699	6.216
B	3.857	2.612	4.428
C	10.022	10.838	-

Table S4.8. Isotopic niche breadth as standard ellipse area (SEAc, ‰^{2}) for bat populations at all 8 sites across three sample years., calculated when be obtained >= 5 samples of conspecifics at a given site.

Site	Species	SEAc 2015	2016	2017
B	Hice	0.656	0.576	2.53
B	Keha	0.79	-	-
B	Kein	0.576	0.828	2.955
B	Rhse	0.17	0.854	-
B	Rhtr	0.264	0.344	-
C	Hice	0.45	0.473	1.141
C	Keha	0.791	-	-
C	Kein	0.655	-	-
C	Rhbo	1.137	-	-
C	Rhtr	0.98	-	-
D	Hidy	0.913	-	-
D	Keha	0.599	2.111	-
D	Kein	0.934	0.612	-
D	Rhtr	0.575	-	-
E	Hice	0.118	1.706	-
E	Hidy	-	0.944	-
E	Keha	0.613	0.77	-
E	Kein	0.648	2.544	-
E	Rhse	0.133	0.649	-
E	Rhtr	0.438	2.461	-
F	Hice	2.027	-	-
F	Hidy	2.476	-	-
F	Keha	2.177	-	-
F	Kein	0.707	-	-
LFE	Hice	1.319	0.539	0.241
LFE	Keha	1.863	-	1.542
LFE	Kein	0.863	0.607	0.99
LFE	Kepa	1.666	-	0.534
LFE	Rhse	1.259	1.473	0.841
LFE	Rhtr	1.113	0.455	-
DVCA	Hice	-	2.151	0.793
DVCA	Keha	-	0.541	0.508
DVCA	Kein	-	4.127	1.737
DVCA	Kepa	-	-	1.003
DVCA	Rhse	-	2.882	-
DVCA	Rhtr	-	2.056	0.654
MBCA	Hice	-	0.56	0.527
MBCA	Hidy	-	0.75	0.356
MBCA	Kein	-	0.659	0.496
MBCA	Kepa	-	1.354	0.449
MBCA	Rhbo	-	0.769	-
MBCA	Rhse	-	0.646	-
MBCA	Rhtr	-	0.435	0.59

Table S4.9. Trophic metrics of each food web at all 8 sites across three sample years. The metrics for each network are mean δ^{15}N, mean δ^{13}C range δ^{15}N, range δ^{13}C range, mean distance to nearest neighbour (MNND), standard deviation of nearest neighbour distance (SDNND), and isotopic variance (‰^{2}; SEAc)

Site	Mean δ^{15}N			Mean δ^{13C}			Range δ^{15}N			Range δ^{13C}			MNND			SDNND			SEAc		
	2015	2016	2017	2015	2016	2017	2015	2016	2017	2015	2016	2017	2015	2016	2017	2015	2016	2017	2015	2016	2017
MBCA		8.42	7.91		-24.57	-24.92		1.04	0.86		0.67	0.79		0.18	0.23		0.02	0.19		0.87	0.70
DVCA		6.96	6.8		-23.71	-25.42		1.12	1.84		1.89	1.74		0.53	0.52		0.62	0.15		3.15	1.38
LFE	10.93	8.55	8.01	-24.64	-24.00	-25.11	1.37	0.94	0.96	0.76	1.08	1.92	0.39	0.57	0.59	0.32	0.06	0.36	1.62	1.12	1.51
B	8.94	7.53	6.32	-24.42	-23.37	-25.08	1.22	0.88	0.12	0.84	0.63	0.76	0.33	0.36	0.77	0.09	0.30	0	1.02	0.92	2.83
C	5.99	6.30	8.40	-24.18	-23.14	-24.44	1.25	0.33	0.04	0.57	0.27	0.96	0.28	0.42	0.96	0.11	0	0	0.95	0.62	1.19
D	9.51	10.25		-23.99	-22.86		1.49	0.13		0.68	0.3		0.53	0.32		0.19	0		1.28	1.51	-
E	8.86	8.84		-24.36	-22.72		1.32	1.93		0.89	1.17		0.41	0.53		0.07	0.43		0.92	2.08	-
F	10.67			-24.56			1.43			1.12			0.71			0.09			2.39		-

Table S4.10. Mean ± SE for each sample year.

Year/Metric	n	Mean δ^{13}C		TP		MNND
2015	29	-24.271 ± 0.073	29	3.657 ± 0.100	6	0.443 ± 0.063
2016	32	-23.607 ± 0.143	32	3.403 ±0.054	7	0.416 ± 0.053
2017	21	-24.993 ± 0.144	21	3.255 ± 0.043	5	0.612 ± 0.123

Table S4.11. Model selection using Akaike information criterion (AIC) on community metrics to evaluate the fixed effects and their interactions. The best models are emboldened, *i.e.* those with the lowest AIC value (ΔAIC = 0) and distinguished from similar models with ΔAIC < 2 (Likelihood ratio test; P < 0.05), or the most parsimonious model when undistinguished.

Model	Fixed component	Random component	AIC	ΔAIC	Log likelihood	P-value
Range $\delta^{15}N$						
2	**Year**	**Site**	**34.4**	**0.00**	-11.316	
3	PC1 + Year	Site	34.6	0.20	-10.479	0.433
1	PC1	Site	36.9	2.50		
4	PC1 * Year	Site	37	2.60		
Range $\delta^{13}C$						
2	Year	Site	26.2	0.00	-9.732	
1	**PC1**	**Site**	**27.5**	**1.30**	**-8.092**	**0.070**
3	PC1 + Year	Site	27.7	1.50	-7.828	0.468
4	PC1 * Year	Site	29.6	3.40		
MNND						
4	**PC1 * Year**	**Site**	**-11.4**	**0.00**		
3	PC1 + Year	Site	-5.9	5.50		
1	PC1	Site	-2.3	9.10		
2	Year	Site	-2	9.40		
SDNND						
1	**PC1**	**Site**	**-5.6**	**0.00**		
2	Year	Site	-3.4	2.20		
3	PC1 + Year	Site	-2.3	3.30		
4	PC1 * Year	Site	1.4	7.00		
SEAc						
1	**PC1**	**Site**	**46.4**	**0.00**	-19.128	
2	Year	Site	48.3	1.90	-18.311	0.442
3	PC1 + Year	Site	50.3	3.90		
4	PC1 * Year	Site	52.6	6.20		

Table S4.12. Model selection using Akaike information criterion (AIC) on bat population metrics to evaluate the fixed effects and their interactions. The best models are emboldened, *i.e.* those with the lowest AIC value (ΔAIC = 0) and distinguished from similar models with ΔAIC < 2 (Likelihood ratio test; P < 0.05), or the most parsimonious model when undistinguished.

Model	Fixed component	Random component	AIC	ΔAIC	Log likelihood	P-value
Trophic position						
11	**PC1 * Year + PC1 * Species**	**Site**	**-28.0**	**0.00**		
12	PC1 * Year + Year * Species	Site	-20.9	7.10		
5	PC1 * Year	Site	-19.1	8.90		
14	PC1 * Species + PC1 * Year + Species*Year	Site	-10	18.00		
8	Year + Species	Site	35.8	63.80		
10	PC1 + Year + Species	Site	37.7	65.70		
2	Year	Site	42.4	70.40		
4	PC1 + Year	Site	44.4	72.40		
3	Species	Site	51.5	79.50		
9	Year * Species	Site	51.5	79.50		
1	PC1	Site	52.8	80.80		
6	PC1 + Species	Site	53.4	81.40		
13	PC1 * Species + Year * Species	Site	61.5	89.50		
7	PC1 * Species	Site	65.1	93.10		
Trophic position						
11	**CH * Year + CH * Species**	**Site**	**-21.0**	**0.00**		
5	CH * Year	Site	-14.4	6.60		
12	CH * Year + Year * Species	Site	-12.1	8.90		
14	CH * Species + CH * Year + Species*Year	Site	-3.1	17.90		
8	Year + Species	Site	35.8	56.80		
10	CH + Year + Species	Site	37.8	58.80		
2	Year	Site	42.4	63.40		
4	CH + Year	Site	44.4	65.40		
3	Species	Site	51.5	72.50		
9	Year * Species	Site	51.5	72.50		
1	CH	Site	52.6	73.60		
6	CH + Species	Site	53.2	74.20		
13	CH * Species + Year * Species	Site	61.2	82.20		
7	CH * Species	Site	65.3	86.30		
Mean $\delta^{13}C$						
11	**PC1 * Year + PC1 * Species**	**Site**	**79.6**	**0.00**		
14	PC1 * Species + PC1 * Year + Species*Year	Site	81.7	2.10		
12	PC1 * Year + Year * Species	Site	82.2	2.60		
10	PC1 + Year + Species	Site	107.7	28.10		

13	PC1 * Species + Year * Species	Site	110.2	30.60		
8	Year + Species	Site	125.2	45.60		
5	PC1 * Year	Site	125.7	46.10		
9	Year * Species	Site	130.7	51.10		
4	PC1 + Year	Site	138.1	58.50		
2	Year	Site	152.3	72.70		
6	PC1 + Species	Site	194.0	114.40		
7	PC1 * Species	Site	199.3	119.70		
1	PC1	Site	203.0	123.40		
3	Species	Site	203.3	123.70		
Niche breadth (SEAc)						
2	**Year**	**Site**	**188.3**	**0.00**	-89.164	0.066
5	PC1 * Year	Site	189.2	0.90	-86.592	0.079
1	PC1	Site	189.7	1.40	-90.856	
4	PC1 + Year	Site	190.3	2.00	-89.135	0.079
3	Species	Site	200.2	11.90		
8	Year + Species	Site	200.8	12.50		
6	PC1 + Species	Site	202.2	13.90		
10	PC1 + Year + Species	Site	202.7	14.40		
11	**PC1 * Year + PC1 * Species**	Site	208.7	20.40		
7	PC1 * Species	Site	211.3	23.00		
9	Year * Species	Site	216.8	28.50		
12	PC1 * Year + Year * Species	Site	217.9	29.60		
14	PC1 * Species + PC1 * Year + Species*Year	Site	224.7	36.40		
13	PC1 * Species + Year * Species	Site	227.2	38.90		
Niche breadth (SEAc)						
2	**Year**	**Site**	**188.3**	**0.00**	-90.638	
1	FC	Site	189.7	1.40	-89.164	0.086
4	FC + Year	Site	190.0	1.70	-89.001	0.568
5	FC * Year	Site	191.6	3.30		
3	Species	Site	200.2	11.90		
8	Year + Species	Site	200.8	12.50		
6	FC + Species	Site	201.7	13.40		
10	FC + Year + Species	Site	202.3	14.00		
7	FC * Species	Site	212.4	24.10		
11	FC * Year + FC * Species	Site	213.0	24.70		
9	Year * Species	Site	216.8	28.50		
12	FC * Year + Year * Species	Site	218.7	30.40		
14	FC * Species + FC * Year + Species*Year	Site	225.0	36.70		
13	FC * Species + Year * Species	Site	225.7	37.40		

Table S4.13. Model selection using Akaike information criterion (AIC) on insect and basal resource metrics to evaluate the fixed effects and their interactions. The best models are emboldened, *i.e.* those with the lowest AIC value (ΔAIC = 0) and distinguished from similar models with ΔAIC < 2 (Likelihood ratio test; P < 0.05), or the most parsimonious model when undistinguished.

Model	Fixed component	Random component	AIC	ΔAIC	Log likelihood	P-value
SEAc Insects						
2	**Guild**	**Site**	**74.093**	**0.00**		
3	PC1 + Guild	Site	76.501	2.41		
4	PC1 * Guild	Site	76.906	2.81		
1	PC1	Site	79.993	5.90		
SEAc Basal Resources						
11	**PC1 * Year + PC1 * Source**	**Site**	**165.2**	**0.00**	-72.618	
12	PC1 * Year + Year * Source	Site	165.4	0.20	-72.702	1.000
14	PC1 * Year + PC1 * Source + Year*Source	Site	166.4	1.20	-72.215	0.324
10	PC1 + Year + Source	Site	167.9	2.70		
6	PC1 + Source	Site	170.4	5.20		
5	PC1 * Year	Site	171.2	6.00		
13	PC1 * Source + Year * Source	Site	171.5	6.30		
8	Year + Source	Site	171.9	0.00		
3	Source	Site	172	6.80		
7	PC1 * Source	Site	172.4	7.20		
9	Year * Source	Site	173.6	8.40		
4	PC1 + Year	Site	173.7	8.50		
1	PC1	Site	176.2	11.00		
2	Year	Site	176.6	11.40		
C_3 leaves C:N ratio						
1	**PC1**	**Site**	**1887.2**	**0.00**		
2	Year	Site	1888.4	1.20	-939.6	
3	PC1 + Year	Site	1890.2	3.00	-939.2	0.3712
4	PC1 * Year	Site	1894.0	6.80		

Table S4.14. Test statistic and P-values for individual terms and interactions from the best models (Tables X – X) of community and population responses of bats as well as lower trophic levels. Non-significant terms and interactions are in grey.

Model	Fixed component	Random component	Term	F	Num DF	Den DF	P
Bat community models							
Range δ^{15}N	Year	Site	Year	2.648	2	10	0.119
Range δ^{13}C	PC1	Site	PC1	0.9767	1	6	0.362
MNND	PC1 * Year	Site	PC1	4.5901	1	12	0.053
			Year	6.8157	2	12	0.011
			PC1: Year	4.1986	2	12	0.041
SDNND	PC1	Site	PC1	0.7216	1	16	0.401
SEAc	PC1	Site	PC1	0.0019	1	5	0.967
Bat population models							
Trophic position	PC1 * Year + PC1 * Species	Site	PC1	0.9572	1	6	0.365
			Year	56.0322	2	57	<0.001
			Species	4.409	7	56	<0.001
			PC1: Year	53.2507	2	53	<0.001
			PC1: Species	0.3408	7	56	0.932
Trophic position	CH*Year + CH* Year	Site	CH	3.5675	1	6	0.104
			Year	33.6236	2	57	<0.001
			Species	1.3431	7	56	0.248
			CH: Year	45.7887	2	57	<0.001
			CH: Species	0.3697	7	56	0.916
Mean δ^{13}C	PC1 * Year + PC1 * Species	Site	PC1	30.1856	1	62	<0.001
			Year	96.7405	2	62	<0.001
			Species	11.7215	7	62	<0.001
			PC1: Year	14.5884	2	62	<0.001
			PC1: Species	1.9437	7	62	0.078
Niche breadth (SEAc)	Year	Site	Year	1.788	2	72	0.175
Other trophic level models							
Insects SEAc	Guild	Site	Guild	0.098	2	11	0.907
Basal resources SEAc	PC1 * Year + PC1 * Source	Site	PC1	0.0009	1	22	0.977
			Year	4.826	2	22	0.018
			Source	7.6452	1	22	0.011
			PC1: Year	3.6821	2	22	0.042
			PC1: Source	0.494	1	22	0.489
C_3 leaves C:N ratio	PC1	Site	PC1	0.3622	1	5	0.5726

Table S4.15. P-values of pairwise t-tests between year-specific averages of dietary metrics, with Bonferroni correction to account for multiple comparisons.

	Year 1	Year 2	*Pc*
MNND	2015	2016	1
	2015	2017	0.426
	2016	2017	0.235
Mean TP	2015	2016	0.039
	2015	2017	0.001
	2016	2017	0.315
Mean δ^{13C}	2015	2016	<0.001
	2015	2017	<0.001
	2016	2017	<0.001
BR SEAc (‰)	2015	2016	1
	2015	2017	0.431
	2016	2017	0.254

Supplementary Figures (Chapter 4)

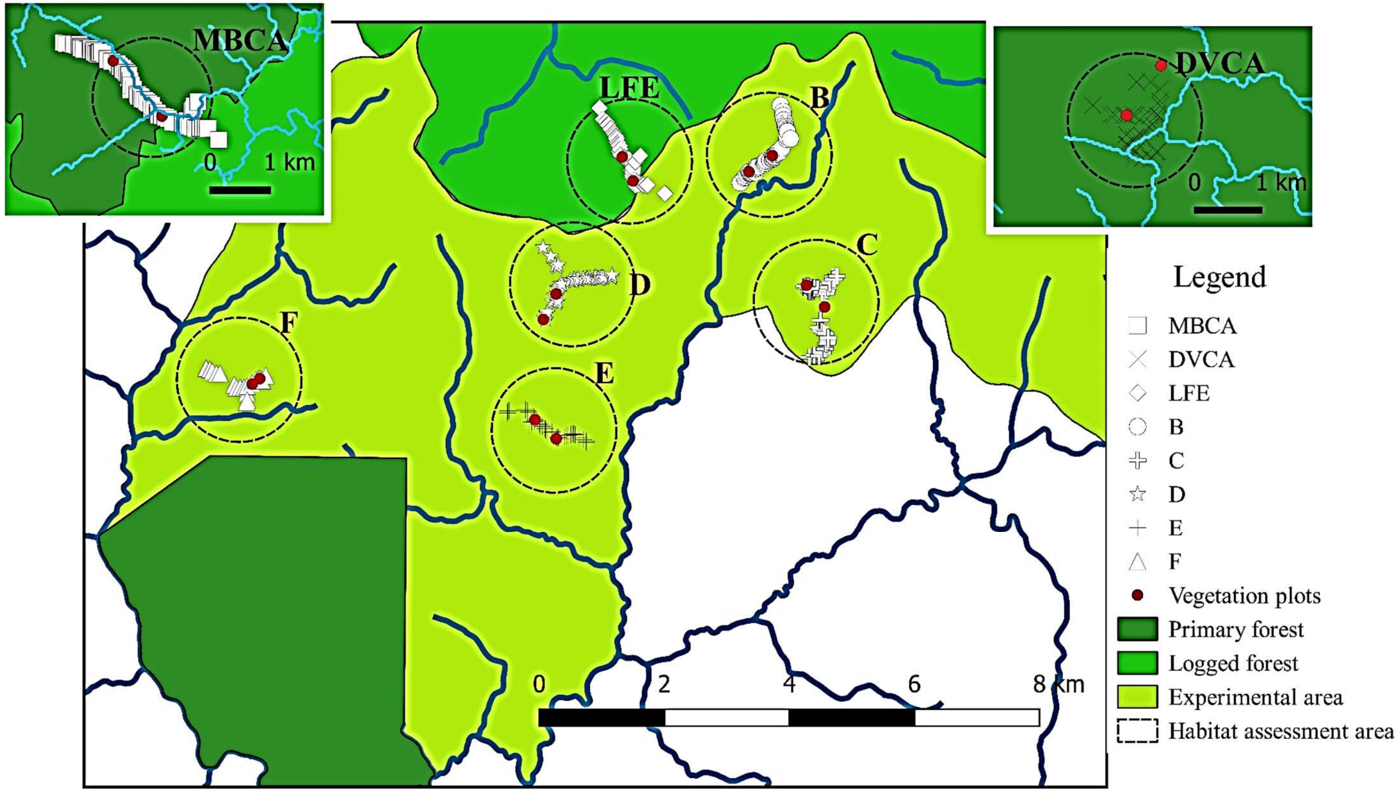


Figure S4.1. Habitat assessment is also shown, representing a 1 km buffer around the mean location of all successful harp traps across three years, weighted by the number of bats caught across all years from the entire ensemble of insectivorous bat species.

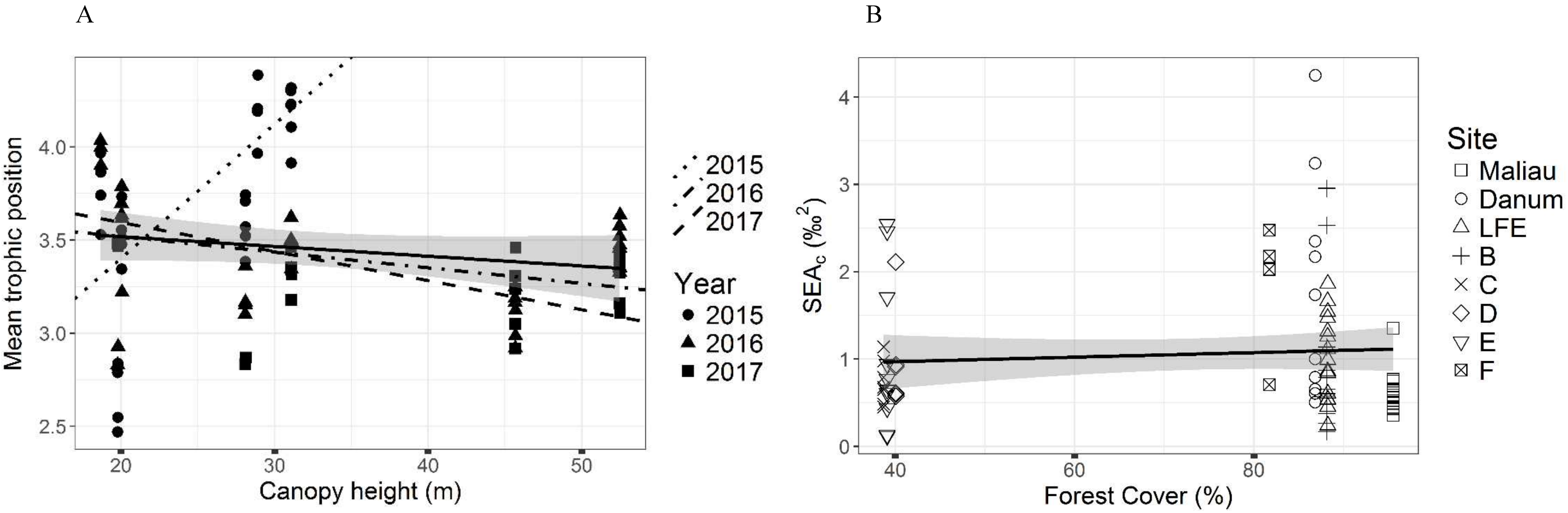


Figure S4.2. Relationship between [A] trophic position and canopy height, and [B] isotopic niche breadth of bat populations, (SEAc ‰^{2}), and forest cover (%). For [A] the symbols show food web metrics calculated at each site for three different years (circle = 2015; triangle = 2016, and square = 2017). The solid line is the global relationship and the shaded area is ± 1 standard error. The additional lines represent the modelled relationship for each year (dotted = 2015; dot-dash = 2016, and dashed = 2017). For [B] the symbols identify SEAc calculated for different sites. The solid line is the modelled relationship, including all three years of data, and the shaded area is ± 1 standard error.

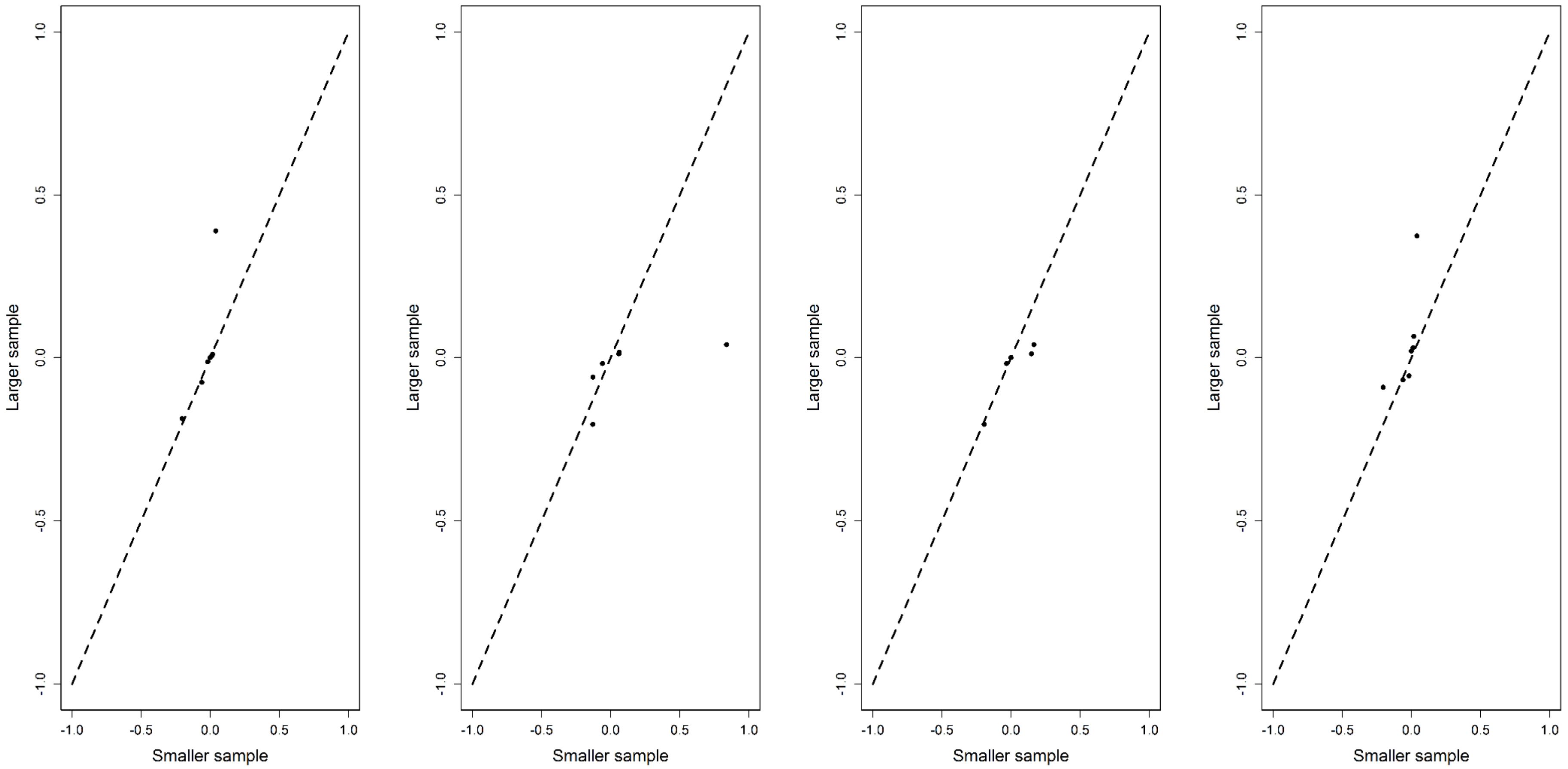


Figure S4.3. Q-Q plots comparing the distributional shapes of the species-specific shifts in isotopic space from 2015 to 2016 of Secondary forest (LFE) to disturbed secondary forest sites [b] B, [c] C, [d] D and [e] E. The origin (0, 0) in each plot corresponds to where the median directions of the two samples coincide. The number of points appearing in each Q-Q plot is equal to the size of the smaller of the two samples.

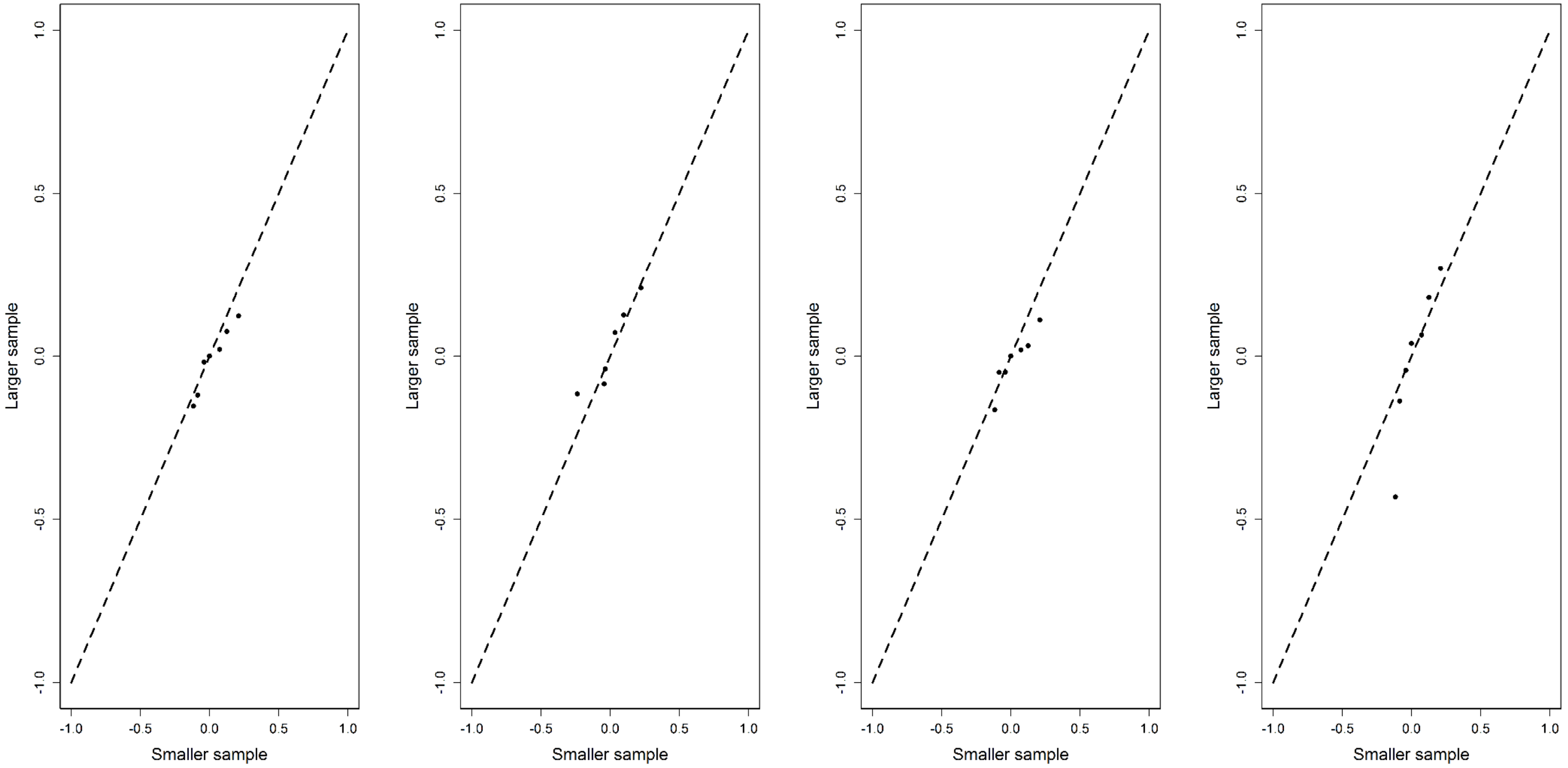


Figure S4.4. Q-Q plots comparing the distributional shapes of the species-specific shifts in isotopic space from 2016 to 2017 of Primary forest (Danum Valley) to [a-b] disturbed secondary forests sites B and C, [c] secondary forest site LFE, and [d] primary forest (Maliau). The origin (0, 0) in each plot corresponds to where the median directions of the two samples coincide. The number of points appearing in each Q-Q plot is equal to the size of the smaller of the two samples.

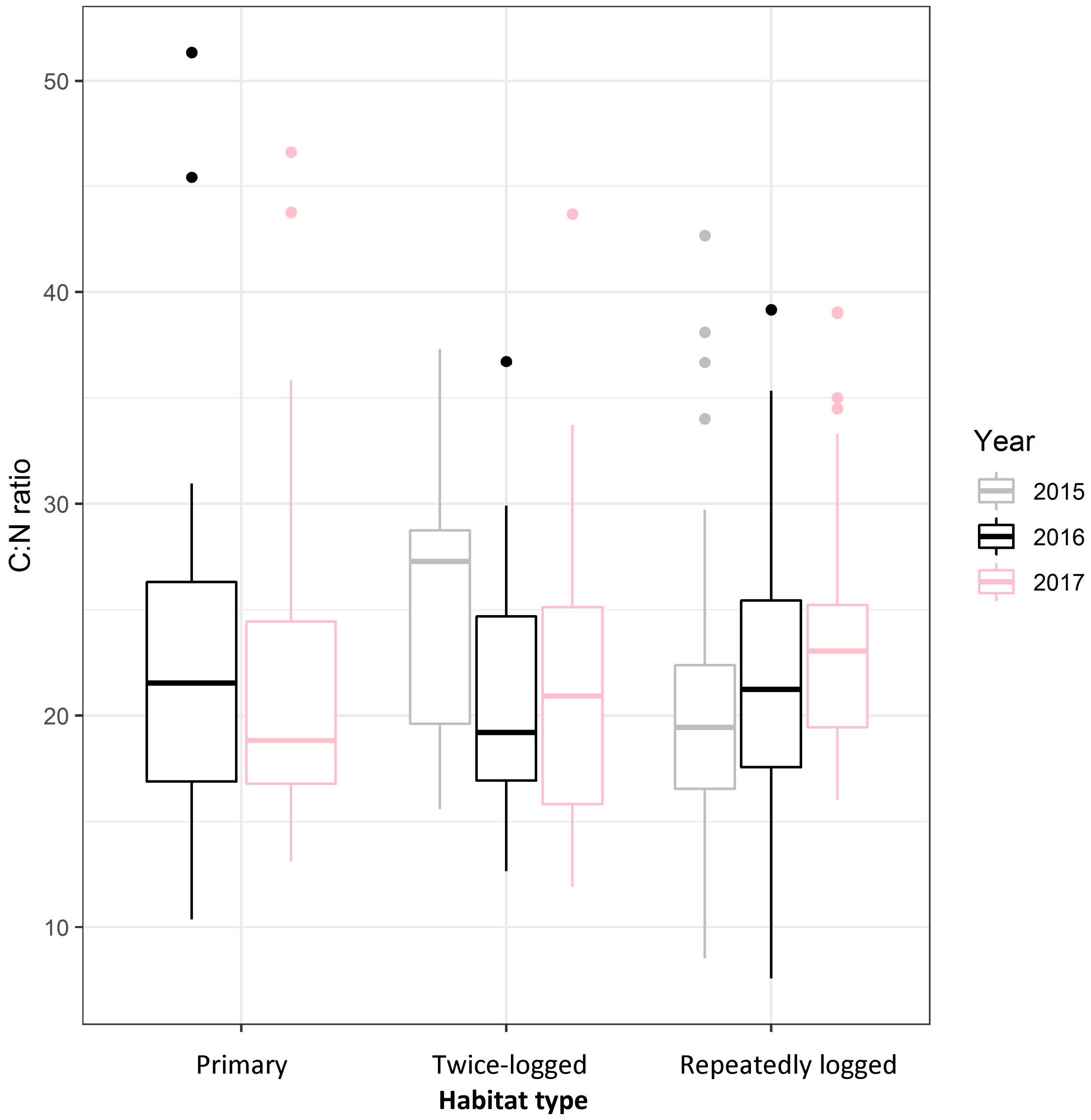


Figure S4.5. Between years and between-habitat differences in C: N ratio of C_3 leaves. No comparisons are significant.

CHAPTER 5

The role of dung beetles in nitrogen recapture in tropical forest soils

Mesocosms set-up, logged-forest site

Abstract

Understanding the mechanisms governing nutrient cycling in the tropics is critical for safeguarding ecosystem productivity and assessing the influence of anthropogenic change in human-modified landscapes. The role of soil meso- and macrofauna for nutrient cycling is well recognised. Dung beetles are important for numerous ecosystem functions, which contribute to soil fertilisation, an important service in both natural and agricultural ecosystems. However, our understanding of the role that dung beetles play in soil fertility and plant-available nutrients remains limited in the tropics. Here, I describe a new method for dung labelling, which is both affordable and can be traced through multiple nitrogen pools into aboveground plant biomass. I investigate the role of dung beetles in assimilation of dung-derived nitrogen (DDN) by aboveground biomass, and aim to detect underlying ecosystem-specific (logged forest and oil palm) nutrient dynamics. I found evidence for differential nutrient cycling in the two ecosystems, affecting rates of either (i) nitrogen mobilisation or (ii) assimilation into plant material. In tropical logged forest I found that assimilation of DDN by seedlings commenced approximately 20 days after first exposure to dung, and that dung beetle presence reduced the assimilation of DDN into plant biomass across the duration of the experiment. However, in the presence of dung beetles, DDN was both more prevalent and more quickly incorporated into the soil matrix. In the oil palm ecosystem, I found no difference in DDN assimilation by seedlings over time regardless of dung beetle presence. Our study suggests a new labelling method for mammalian dung, allowing assessment of the impacts of dung beetles on nitrogen cycling and associated biological processes in the tropics. However, the differences in ^{15}N assimilation between oil palm and logged forest suggests that both labelling requirements, and underlying nutrient dynamics, are ecosystem specific.

Introduction

The efficiency with which recaptured nutrients are made available to primary producers has implications for ecosystem productivity, especially in the often nutrient limited tropics (Swift *et al.* 1998). While empirical evidence shows decomposition is directly the result of microbial activity (Bernabé *et al.* 2018), the importance of soil fauna is increasingly recognised (Cole *et al.* 2006). Soil meso- and macrofauna affect microbial biomass (Bradford *et al.* 2002) and levels of microbial activity (Mahendrappa *et al.* 1986; Slade *et al.* 2015), largely determined by effects upon organic input quality (Gonzalez & Seastedt 2001; Cole *et al.* 2002; Hobbie & Villéger 2015) and soil physical structure (Beynon *et al.* 2015).

Dung beetles (Coleoptera: Scarabaeoidea) are a specialist component of the soil macrofauna, and play a key role in the processing of nutrient-rich animal dung in diverse terrestrial systems (Nichols *et al.* 2008). Previous work has focused on easily quantified functions such as burial of dung (*e.g.* Slade et al. 2011; Dangles et al. 2012), or seeds (*e.g.* D'hondt et al. 2008; Santos-Heredia & Andresen 2014), and therein clearly highlighted the relevance of dung beetles in tropical as well as temperate forests. In tropical forests of South East Asia wild cattle often remain fairly abundant, and elephants and wild boar add to the dung production in these natural systems. However, the effects of dung beetle activity on ecosystem functioning and services remains poorly understood (*e.g.* Beynon et al. 2015). While, recent studies have to some extent revealed the importance of dung beetle activity for nutrient cycling (Manning et al. 2016; Forgie et al. 2018), and engineering of soil structure (Brown *et al.* 2010), our understanding of the role that dung beetles play in soil fertility and plant-available nutrients remains limited, particularly in the tropics (Nichols *et al.* 2008).

Nitrogen cycling is important in regulating primary productivity in many ecosystems (Pajares & Bohannan 2016). Losses of N are predominantly via ammonia (NH_3) volatisation, leaching, and denitrification (Cameron et al. 2013). Dung beetles prevent the loss of dung-derived nitrogen (DDN) via NH_3 volatisation by burial of the dung under the soil surface (Nichols et al. 2008). Furthermore, in temperate ecosystems, dung beetle activity has been shown to influence a number of processes regulating nitrogen availability to plants, including increased transport of DDN into the soil, and its uptake by plants (Nervo et al. 2017). The positive effect of dung beetles on assimilation of DDN is thought to be due to facilitative effects, for example increased microbial activity (Slade *et al.* 2015), and therefore the acceleration of bacteria-mediated nitrogen mineralization rates (Nervo *et al.* 2017). In addition, dung beetle activity increases carbon and nitrogen levels in the upper soil layers, facilitating bacterial growth (Yokoyama et al. 1991). However, the regulatory processes acting upon nitrogen cycling in tropical soils are likely to be distinct from temperate processes due to differences in biotic and abiotic characteristics between the two systems (Foster & Bhatti 2006). Owing to the increasing focus on dung beetle ecology (Nichols *et al.* 2008) and in particular the provision of ecosystem functions and services (Beynon *et al.* 2015), this group offers a powerful tool to further investigate the role of detritivores in tropical soils, and specifically the routing of nitrogen contained within mammalian dung to aboveground productivity.

Anthropogenic influence upon nitrogen cycling has been a focus over past decades (Swift *et al.* 1998; Lavelle *et al.* 2005), including shifts in regulatory processes between natural and agricultural ecosystems (Tscharntke *et al.* 2012). Despite this, the response of processes regulating nitrogen cycling to land use change is still in its infancy (Pajares & Bohannan 2016). Cultivation of oil palm plantations is expanding in tropical regions (Fitzherbert et al. 2008), and there are calls to better understand the maintenance of ecosystem functions in conversion landscapes (Lewis 2009; Dislich *et al.* 2017). Cattle are regularly grazed in oil palm (Slade *et al.* 2014 and refs therein), raising interesting questions regarding the potential for reduced fertiliser inputs. Detailed understanding of nutrient cycling in oil palm plantations, and the relationship with land-use change could thus inform management of human-modified landscapes.

The use of nitrogen-15 (^{15}N) enrichment studies has improved our understanding of nitrogen cycling in soil, plants, and food webs (Barraclough 1991; Ngai & Srivastava 2006; Nervo *et al.* 2017). The ^{15}N content of substrates including soil inorganic-nitrogen, plants, gases, and excreta can be enriched in order to trace the fate of component N compounds in the environment (Clough *et al.* 2013). The labelling of vertebrate faeces with ^{15}N can be achieved through feeding cattle ^{15}N-enriched forage (Powell *et al.* 2004) or incubation of dung organic matter with the dissolved ^{15}N-compound (Nervo *et al.* 2017). However, labelling of forage can be prohibitively expensive as it involves applying costly tracer to a substantial area of crop, while incubation of dung with a dissolved tracer may lead to unrealistic nitrogen mobility as it does not achieve true incorporation of the labelled compound into the dung matrix. The latter has the potential for misleading outcomes in the comparison of treatment effects on the mobilisation of nutrients from vertebrate dung over time, especially in tropical systems where leaching of nutrients is increased due to high rainfall.

Here, I developed a novel method to incorporate a ^{15}N-tracer into cattle dung, which did not require expensive labelling of forage, but nonetheless facilitated tight incorporation into the dung matrix. I then used a mesocosm experiment to track the fate of DDN using three treatments, (a) *soil only control*, (b) *dung only*, and (c) *dung + dung beetles*, in order to assess whether the presence of dung beetles facilitates N assimilation by aboveground biomass, both in terms of rate of uptake and peak uptake. I conducted the experiment in two different ecosystem types, logged forest and oil palm plantation, in order to investigate differences in N cycling between the two systems. Focusing on the tunneller guild of dung beetles, which bury dung below the soil surface, I provide a preliminary understanding how dung beetle colonisation of dung pats temporally effects movement through the soil column and assimilation of DDN by plants. Specifically I aimed to ascertain (i) whether the level of ^{15}N labelling achieved from our novel labelling method is sufficient to be tracked through multiple dilution pools, *i.e.* soil biomass of open-bottom mesocosms, and biomass of the plant; (ii) the time period over which dung-derived nutrients are made available to aboveground biomass in a tropical soil context, and at which point assimilation peaks, (iii) how the presence of dung beetles affects the assimilation rate of DDN over the experimental period, (iv) whether I can detect differences in soil $\delta^{15}N$ between treatments, and (v) more specifically whether depth has an effect upon treatment differences, owing to differential quantities of dung burial at different depths through the soil vertical profile.

Methods

Study site

I conducted the study in two different ecosystem types in Sabah, Malaysian Borneo (Fig. S5.1): continuous twice-logged lowland dipterocarp forest located inside the Stability of Altered Forest Ecosystems (SAFE) project, a 7200 ha experimental landscape (Ewers *et al.* 2011), and an oil palm plantation within the Menggaris Estate of the Benta Wawasan oil palm company, planted 2009 – 2012 and located approximately 17 km from the SAFE project site. The oil palm site undergoes regular fertilisation, with a nitrogen, phosphorus, and potassium mixture, and the last application was three months prior to the experimental start date. I set up eighteen mesocosms in each ecosystem type, with six replicates of each of our three treatments (i) *soil only control*, (ii) *dung only*, and (iii) *dung + dung beetles* (Fig.5.1).

Dung 15N labelling and processing

I labelled experimental dung with ^{15}N so that the fate of the constituents could be traced through the soil profile and into aboveground biomass (experimental seedlings). Administration of ^{15}N-labelled tracer into the drinking water of cattle facilitated incorporation of the label into the faecal matrix. I aimed to achieve ^{15}N-enrichment of dung that would provide a signal above the isotopic variation within soil endogenous nitrogen, for which enrichment would naturally occur through fractionating pathways (*i.e.* altering the ratio of ^{14}N and ^{15}N isotopes).

To produce labelled dung I used a local farm in Kalabakan, Tawau (supplementary Fig. S5.1). The farm is ~125 ha, consisting of oil palm *(Elaeis guineensis)* inter-grazed by a herd of 15 Brahmin cattle, to which wormer medication is administered every six months. For labelled dung production, two Brahmin cattle, one male and one female (non- or post-reproductive), each weighing approximately 300 kg were stalled for 71 hours in June 2016 and fed a diet of mature oil palm leaves.

I made a 600 µM solution of ^{15}N-ammonium by mixing 2 g of 95 atom% $^{15}NH_4Cl$ with 60 L of local rain water. I presented this solution to the cattle in equal measures across two water pails and samples were taken to verify the concentration (T_0). I refilled the pails to 60L at T_{24hr} and T_{48hr} presenting an increasingly diluted ^{15}N-ammonium solution (see supplementary Tables S5.1 for concentrations). The ammonium (NH_4) concentration of the diluent rainwater would have been insignificant compared to that of the rumen, given the extent of anaerobic microbial processes in the rumen converting organic matter to ammonia (Nolan & Dobos 2007). All other water sources were unavailable to the cattle for the duration of the experiment. Previous studies have found that ^{15}N labelling of cattle dung via direct administration, *i.e.* not incorporated into forage, peaks at approximately 50 hours post administration (Powell et al. 2004; Kemp et al., unpublished). Therefore, to retrieve sufficient dung for our experiment I sampled across a 10-hour window around T_{50}. I collected excreted dung and stored it in a 25 L bucket for a maximum of 12 hours before used in the mesocosms. Using this method, the dung was enriched to 50 ± SE 0.171 ‰ (n = 4) for the logged forest experiment and 46 ± SE 0.344 ‰ (n = 4) for the oil palm experiment (see supplementary Fig. S5.2 for enrichment over time). I thoroughly homogenised the dung and then divided it into 12 dung patties of ~ 300 g for each ecosystem type. See supplementary methodology 5.1 for full details of processing and weights.

Dung beetle collection

I collected dung beetles of the paracoprid nester (tunneller) guild in order to populate the dung beetle treatment. I collected beetles from the same ecosystem type as they would be placed during the experiments, *i.e.* logged forest or oil palm plantation. Beetles were collected using live human-dung baited pitfall traps, which capture a representative community in the beetles in these ecosystems (Slade et al. 2011). Traps were constructed from 1.5 L plastic bottles cut in half with the top half inverted to form a funnel. Traps were dug into the ground so the rim was flush with the soil surface, and leaves and soil placed in the bottom, with small drainage holes, and covered with a plate as a rain shield. Twelve traps were baited on 7th June in logged forest, and on 15th June in oil palm, and left for 24 hours. I collected beetles into plastic boxes, and sorted to species on return to the lab. Beetles were stored in single species, mixed sex boxes with damp tissue, and kept in a dry, cool, room with natural daylight for a maximum of 7 days before placing into mesocosms. The day after collection from the field, I fed the beetles a small amount of cattle dung collected from a local herd of cattle grazing in acacia plantation nearby. On subsequent days I gave beetles kitchen roll soaked in liquidised cattle dung. This ensured that all beetles had been fed the same food source prior to the experiment starting, and were not satiated at the start of the experiment.

I investigated how a natural dung beetle community affects the process of nitrogen mobilisation in each of the two ecosystem types. Therefore, rather than standardise biomass or abundance between forest and oil palm I used a standardised community from each ecosystem. Oil palm in the SAFE landscape contains about half the biomass of beetles of logged forest (E. Slade, unpublished data). I assembled beetle communities based on mean relative abundances of species collected from 16 human-dung baited pitfall traps set in logged forest and 18 traps set in oil palm within the SAFE landscape in 2011 (E. Slade, unpublished data; see supplementary Table S5.2 for the communities used to populate mesocosms in each ecosystem type). Only species that had an average abundance in traps in 2011 greater or equal to two were used. Telecoprid nesters (rollers), which roll a ball of dung and bury it away from the dung pat, were not included in communities as their behaviour in mesocosms is altered compared to natural systems (E. Slade, pers. obs.). However, I recognise that the amount of dung mobilised by tunnellers may then be slightly higher than in a full community where the rollers would also remove the dung.

Experimental treatments

I deployed the 18 mesocosms into each of the ecosystem types (logged forest and oil palm) in mid-May 2016, to give the soil one month to recover from the disturbance. I constructed mesocosms from black plastic containers, 40 cm diameter and 25 cm high after removing the base. I dug mesocosms 20 cm into the ground leaving 5cm above the surface. I arranged them in a 6 x 3 grid with a minimum of 3 m between each mesocosm to minimise interaction between the soil nutrients cycling in each mesocosm. As proximity of the seedlings to mature trees may increase competition for nitrogen and other nutrients I recorded the distance of each mesocosm to the nearest mature tree (any species with diameter at breast height > 30 cm) for inclusion in our analyses.

I randomly selected 12 of the mesocosms, to receive ^{15}N-labelled dung patties weighing 300 ± SD 2.27 g in logged forest and 410 ± SD 2.04 g in oil palm. I populated six randomly selected mesocoms from within those 12 treated with dung with standardised dung beetle communities (Fig. 5.1, supplementary Table S5.2). The remaining six mesocosms were left as soil only controls. I covered each mesocosm with a fine nylon mesh secured with a rubber belt to prevent beetles leaving or colonising the mesocosms, and to standardise any microclimatic effects between treatments. However, after 48 hours I opened the dung beetle treatments for a 24 hours period to allow the beetles to emigrate rather than forcing them to artificially stay in the same pat (cf. Roslin 2000; Slade et al. 2017), and then re-covered the mesocosms with netting.

I planted all 18 mesocosms with either Dipterocarpaceae seedlings *Parashorea malaanonan* (Blanco) (logged forest) or a 'Ramet' six-month old oil palm seedlings (Serijaya Industries Sdn. Bhd.) (oil palm). I removed soil within the mesocosm to the depth of the seedling roots, ~15 cm, and placed a seedling in the hole along with its nursery soil, and then repacked the hole with local soil, whilst making sure to leave the growth ridge of the Dipterocapaceae seedlings exposed to the air. In logged forest, dung and dung beetles were added four days prior to the planting of seedlings in order to allow processing of the dung. In the *dung only* treatments (in which dung had not been buried below the surface due to the absence of beetles) I removed the dung prior to digging and replaced it in two halves around the seedling at the soil surface after planting. Mixing of the soil from the 0-15 cm horizons was limited to a minimum during this procedure. However, as I noted some inevitable mixing of the horizons, in the oil palm the seedlings were planted first, and dung and beetle treatments were then applied later the same day to try and reduce soil mixing further.

Leaf and soil sampling, processing, and analysis

I sampled leaves eight times over the eight-month duration of the experiment, with high frequency during the first month, aimed to capture the initial assimilation of DDN into the plants (See supplementary Fig. S5.3 for specific sample days). I collected one leaf from the Dipterocarpaceae or palm seedlings for each sample event. For dipterocarp seedlings I alternated collection of the terminal leaf from top and bottom (leaving the topmost, newest leaf) between consecutive sample days, and for palm seedlings I sampled the two penultimate leaflets from alternating sides of the mid-stem, from the youngest fully formed frond. As assimilated ^{15}N did not plateau in logged forest during the 8-month timeframe of the experiment, I took a sample after 21 months in order to determine whether all DDN had been turned over in the plant biomass after this time. I also sampled soil seven times from logged forest over the course of the experiment (see Fig. S5.3 for specific sampling days). Any remaining surface dung was removed prior to soil sampling, and replaced thereafter, in order to reduce the possibility of contamination. If a soil core was unsuccessful (most likely due to beetle channels) a second core was taken directly beside. On each sample day, a core of 10cm depth was taken and split into vertical horizons 0- 2cm, 2-5 cm and 5-10cm.

The leaf and soil samples were dried at 60°C for a minimum of 48 hours (Hyodo *et al.* 2010). I then ground samples to a fine powder using a ball mill (Retsch UK Ltd., Hope, UK). I weighed ground samples into 6 x 4 mm ultraclean tin capsules (Elemental Microanalysis Ltd., Okehampton, UK) using an ultra-microbalance with readability 1 µg

(Mettler-Toledo, Greifensee, Switzerland) to provide sufficient elemental carbon and nitrogen for analysis by continuous flow isotope ratio mass spectrometry (SERCON, Crewe, UK). Isotope ratio was expressed in per mil (‰) relative to the international reference standard ($R_{standard}$) atmospheric nitrogen. I calculated the isotope value for sample $\delta^{15}N$ as:

$$\delta^{15}N = \left(\frac{\left(\frac{^{15}N)}{^{14}N}\right)sample}{\left(\frac{^{15}N)}{^{14}N}\right)standard} - 1 \right) \cdot 1000 \text{ ‰}, \qquad \text{(Eq.1)}$$

Where ^{15}N and ^{14}N are signals for *m/z* 28 and 29, respectively. I then converted values from $\delta^{15}N$ to ^{15}N atom %:

$$^{15}Natom\% = 100 \cdot \frac{\delta^{15}N+1000}{\delta^{15}N+1000+\left(\frac{1000}{0.003676}\right)} \qquad \text{(Eq. 2)}$$

I calculated excess ^{15}N in atom % over natural abundance by subtracting an ecosystem-specific baseline value. I used ecologically relevant baselines for the two sample types: the foliar baseline was calculated as the mean ^{15}N in atom % across all seedlings at D_0 (*i.e.* before planting), and the soil baseline was calculated as the mean soil ^{15}N in atom % across all mesocosms at D_1 (taken after planting, and therefore accounting for any disturbance of soil profile during planting). Excess ^{15}N was then used to calculate the mass of new ^{15}N assimilated into leaves per mass of carbon, hereafter assimilated ^{15}N, and the mass of ^{15}N incorporated into soil matrix, hereafter soil ^{15}N:

$$Ex\mu g^{15}N \cdot \mu gC^{-1} = \frac{\left(\frac{Ex^{15}N\ atom\%}{100} \cdot \mu gN\right)}{\mu gC} \qquad \text{(Eq. 3)}$$

Statistical analyses

All analyses are performed in R 3.5.1 (R Development Core Team 2018). I used generalised least squares (gls) models in nlme (Pinheiro et al. 2018) to test the effect of treatment and experimental day on the response variables, assimilated ^{15}N and soil ^{15}N. These tests allowed us to assess whether the ^{15}N label of dung was sufficient to allow traceability in the leaves and soil, respectively. To optimize the models I conducted stepwise reduction from the maximal model, including all terms and interactions, using Akaike information criterion (AIC) (see supplementary Tables S5.3 & S5.4 for logged forest and oil palm assimilation, respectively and S5.5 for logged forest soils). I used restricted maximum likelihood (REML) and maximum likelihood (ML) estimation of model parameters when optimizing the fixed and random components respectively.

Due to the heteroscedasticity of the residual variance, for logged forest leaf data, I also incorporated heterogeneity into the random component of the model (Zuur et al. 2009) by including the exponential variance function, varExp (Zuur et al. 2009). Data from logged forest soil and oil palm leaves met the assumptions of normality and homoscedasticity of the residuals, and I therefore only optimized the incorporation of the random effect, mesocosm ID. When modelling the response of assimilated ^{15}N and soil ^{15}N, I included distance to nearest mature tree (> 30 cm DBH) as a covariate in the maximal model in order to check for an interactive effect upon the response. When modelling the response of soil ^{15}N I also included vertical depth as a covariate in the maximal model in order to test for an effect of depth upon treatment differences.

Finding a significant interaction between Treatment and Experimental day upon assimilated ^{15}N, I employed post-hoc tests to detect where differential responses lay. In order to strengthen our understanding of label traceability, I first explored differences in assimilated ^{15}N by seedlings exposed to the two experimental treatments compared to the soil only control. I conducted pairwise comparisons between control and dung-receiving treatments using the 'lsmeans' package (Lenth 2016); p-values were estimated using the Tukey test. Furthermore, under the assumption that thorough homogenisation of dung provided uniform $^{15}NH_4+$: $^{14}NH_4+$ across the dung-receiving treatments, I compared uptake rates of DDN between dung-receiving treatments, and thereby identified the impact of dung beetle presence on the assimilation of DDN over time. In compliment, by visual comparison to the soil only control I estimated the approximate time at which seedlings began to assimilate dung-derived ^{15}N in the experimental treatments, and whether this was different given the presence and absence of dung beetles. Finally, I used repeated measures ANOVA to test whether the assimilated ^{15}N at > 1 year (21 months) was different to the D0 baseline, for seedlings which were still alive, whilst accounting for the nested structure of mesocosm identity within experimental day.

Results

Only 11 of the 18 dipterocarp seedlings (3 x soil, 4 x dung and 4 x dung + beetle treatments) had a sufficient number of leaves to sample at the last event. At the end of the experiment all palms had a sufficient number of leaves to sample, permitting full representation across the whole sampling period. Thus the logged forest dataset contained 137 data points and the oil palm contained 144 data points across the 8 sampling events and 18 mesocosms. For the post-experimental sample in logged forest, taken 21 months after commencement, n = 10 following a further seedling death.

The fixed structure of the best models explaining assimilated ^{15}N by seedlings in logged forest and oil palm were both $^{15}N \sim Treatment*Day$. There was a significant interactive effect between experimental day and treatment on assimilated ^{15}N in both logged forest (GLS, treatment x experimental day, $F_{2,131} = 13.813$, $P < 0.0001$) and oil palm (GLS, treatment x experimental day, $F_{2,136} = 16.79$, $P < 0.0001$) ecosystems (Fig. 5.3). In logged forest there was a significant difference in the assimilation of DDN over time in the *soil only control* compared to experimental dung treatments, with and without beetles (Tukey post hoc test, $P = 0.006$ and $P < 0.0001$, respectively, Fig. 5.3A). However, in oil palm there were no such differences between the control and the dung-receiving treatments (Tukey post hoc test, $P > 0.05$. Fig.5. 3B).

In logged forest there was a significant difference in the assimilation of DDN over time between dung-receiving treatments (Tukey post hoc test, $P = 0.048$, Fig.5.3A), with less assimilation of DDN when dung beetles were present. However, in oil palm there was no significant difference in the assimilation of DDN over time with the presence of beetles (Tukey post hoc test, $P > 0.05$, Fig. 5.3B). The overlap of 95 % confidence intervals around the modelled lines (Fig. 5.3A) show that the dung-receiving treatments began to diverge from the *soil only control* in logged forest at approximately day 20, *i.e.* at this point uptake of DDN is evident within the leaf tissue. Finally, I found that the assimilated ^{15}N in logged forest seedlings remained significantly higher than the D_0 baseline (repeated measures ANOVA, $F_{1,10} = 11.094$, $P = 0.0126$, $n = 20$) even after 21 months, but there was no interaction between day and treatment (repeated measures ANOVA, $F_{2,10} = 0.343$, $P = 0.721$).

I lost a single soil sample (D_{14}, dung only, depth 2- 5 cm) prior to laboratory analysis, thus providing 377 samples. Although the elemental nitrogen content of many samples fell below the threshold for stable $\delta^{15}N$ values, there was no significant relationship between $\delta^{15}N$ and μg elemental nitrogen (See supplementary methodology 5.2). However, I took the measure of removing the two observations representing the minimum and maximum $\delta^{15}N$ values (D_{21}, dung only, depth 0-2 cm; D_{43}, dung only, 5-1-0 cm) in order to reduce the potential for spurious results. Thus, the final dataset of soils consisted of 375 samples. The fixed structure of the final model was $^{15}N \sim Treatment*Day + Treatment*Distance\ to\ nearest\ mature\ tree$. There was a significant interaction between treatment and day (GLS, treatment x day, $F_{2,367} = 3.534$, $P = 0.0302$; Fig. 5.3). There was also a significant interaction between experimental treatment and distance to the nearest mature tree (GLS, treatment x distance, $F_{2,367} = 5.834$). Soil was more enriched in ^{15}N in the experimental treatments compared to the *soil only control*. The treatment containing dung beetles was initially enriched compared to both other treatments, remaining higher for the duration of sampling. However, the *dung only* treatment increased to the same level as the beetle containing treatment after approximately 50 days. The interaction between experimental day and distance from the nearest mature tree was retained in the final model according to AIC-based simplification, but was not significant (GLS, $F_{1,367} < 0.001$, $P = 0.9967$). The covariate depth did not improve the model fit and was therefore excluded from the final model.

Tables and Figures

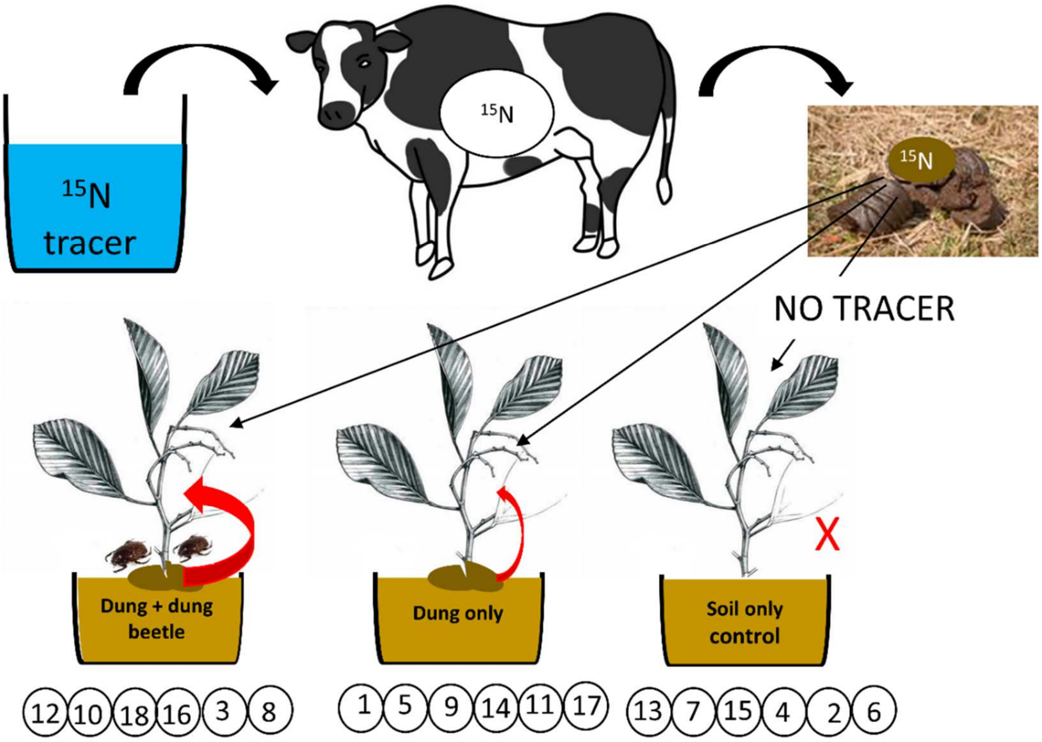


Figure 5.1. Depiction of the dung labelling method and the experimental design. A 600 μM solution of ^{15}N-ammonium was made by mixing 2 g of 95 atom% $^{15}NH_4Cl$ with 60 L of local rain water. This solution was presented to the cattle while all other drinking sources were unavailable for 50 hours. Dung voided across a 10-hour window around 50 hours after first exposure to the ^{15}N-labelled water was collected, homogenized and added to the experimental mesocosms as dung pats weighing 300 ± SD2.27 g (n = 12) in logged forest and 410 ± SD 2.04 g (n=12) in oil palm. Using this method, the dung was enriched to 50 ± SE 0.171 ‰ (n = 4) for the logged forest experiment and 46 ± SE 0.344 ‰ (n = 4) for the oil palm experiment. Red arrows show our predictions for treatment differences in the assimilation of DDN. Circled numbers depict unique identities for all mesocosms.

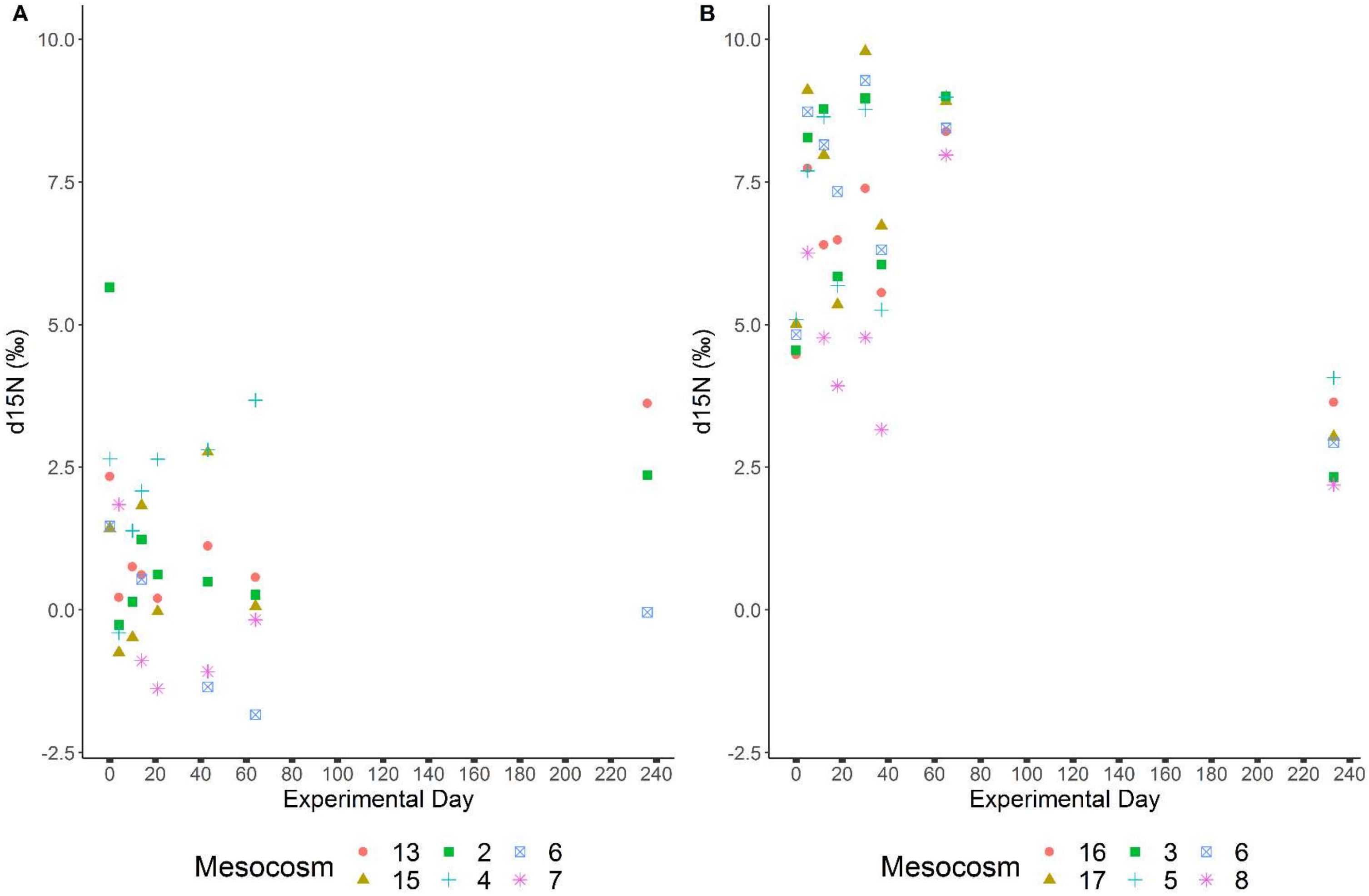


Figure 5.2. Foliar ^{15}N across time in [A] logged forest, and [B] oil palm for six different *soil only control* mesocosms at any given day.

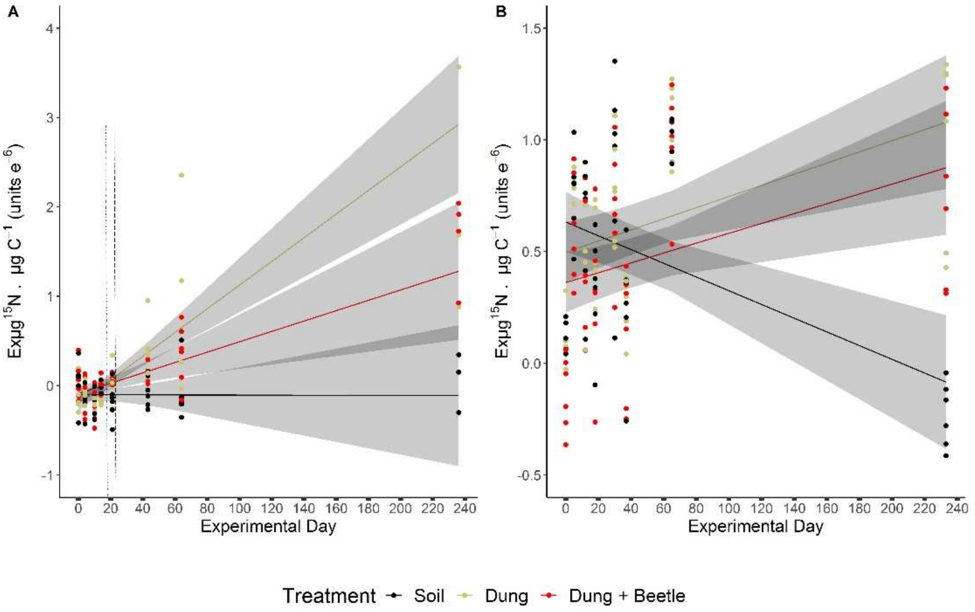


Figure 5.3. Predicted models for the response in assimilated ^{15}N assimilated per mass of carbon, $Ex\ \mu g^{15}N \cdot \mu g\ C^{-1}$, across time for the three treatments in [A] logged forest (GLS, treatment x experimental day, $F_{2,125} = 12.17$, $P < 0.0001$) and [B] oil palm (GLS, treatment x experimental day, $F_{2,136} = 16.16$, $P < 0.0001$) with 95 % confidence intervals. The two graphs are on different scales. Points represent the raw data for individual mesocosms. Dotted lines indicate where the confidence intervals begin to separate from the modelled relationship for *soil only control*, *i.e.* where assimilation of dung-derived nitrogen begins (·-·-·-·-·-·-·) in the presence of *dung only*, and (------) in the presence of *dung* + *dung beetles*. Excess ^{15}N was calculated by subtraction of natural abundance ^{15}N, calculated as the mean foliar ^{15}N (in atom %) across all seedlings at D_0, *i.e*. before they had been planted in the ^{15}N-labelled dung-soil matrix (or soil matrix for *soil only control*).

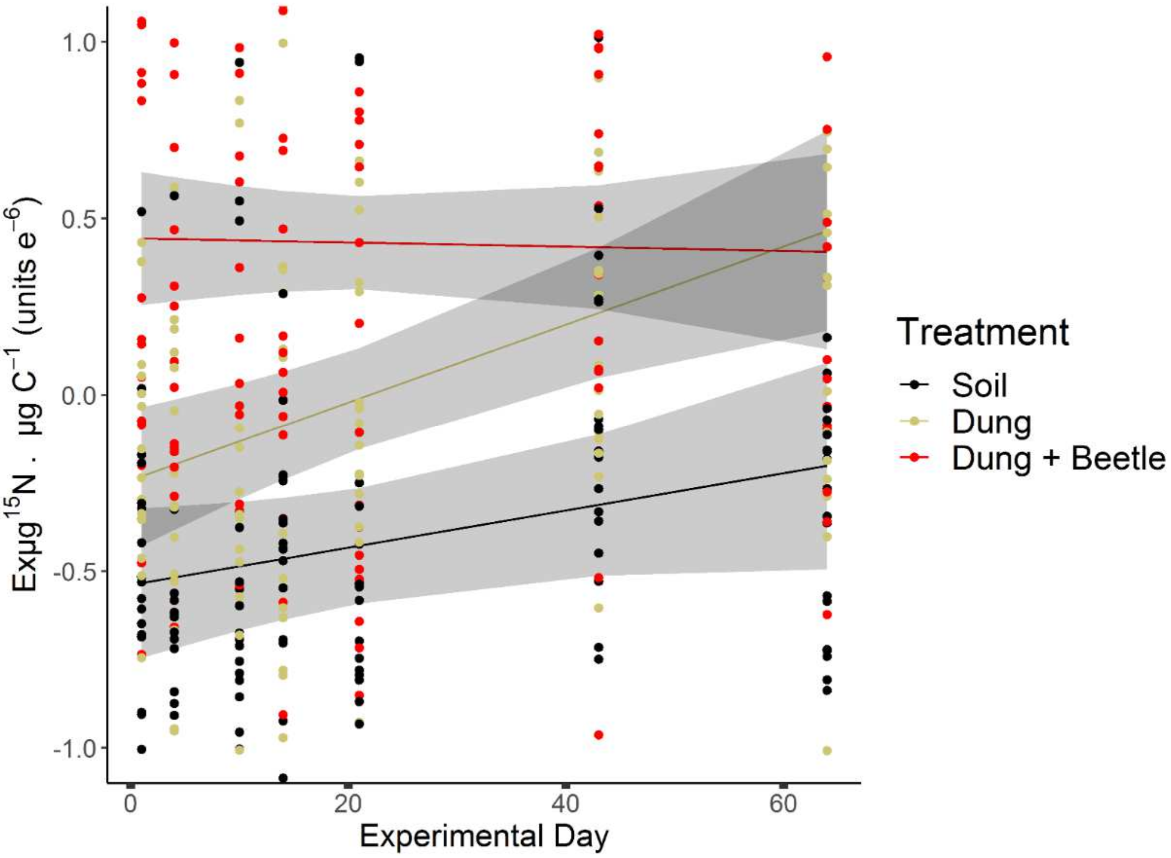


Figure 5.4. Predicted model for the response of soil ^{15}N per mass of carbon, *(log) Ex µg* $^{15}N \cdot \mu g\ C^{-1}$, across time at all three depths for the three treatments in logged forest (GLS, $F_{2,361} = 31.502$, $P < 0.0001$) with 95 % confidence intervals. Points represent the raw data for individual mesocosms across all depths. Excess ^{15}N was calculated by subtraction of natural abundance ^{15}N, calculated as the mean soil ^{15}N (in atom %) across all mesocosms at D_1, *i.e.* after planting of seedlings.

Discussion

Our new method of dung labelling achieved ^{15}N-enrichment that was sufficient to trace through multiple nitrogen pools into aboveground plant biomass. However, the among-treatment differences in ^{15}N assimilation between oil palm and logged forest suggest that both labelling requirements, and underlying nutrient dynamics, are ecosystem specific. For seedlings planted into logged forest I found two results which were contrary to previous studies. Firstly, assimilated ^{15}N increased in seedlings exposed to dung only after a considerable time (approximately 20 days). Secondly, dung beetle presence reduced the assimilation of ^{15}N over time. However, as expected dung beetles increased the rate at which dung was incorporated into the soil matrix, especially in the first month of the experiment. In comparison to our results in logged forest, there was no difference in ^{15}N assimilated into leaves with or without dung beetles present in the oil palm ecosystem.

Efficacy of ^{15}N labelling of dung

In both logged forest and oil palm I observed variation in foliar ^{15}N for the *soil only control seedlings* across the duration of the experiments (Fig 5.2). The variation could result from analytical imprecision as I measured small ratios of ^{14}N:^{15}N. . Despite background noise, in logged forest I was able to detect incorporation of DDN in the soil matrix and the commencement of DDN assimilation by dipterocarp seedlings. However, this was not the case in the oil palm ecosystem. In logged forest the assimilation of ^{15}N for the two dung-receiving treatments increased substantially beyond the upper limit of the *soil only control* (Fig.5.3A). In comparison, between-treatment differences in oil palm were driven by a decline in the baseline values (Fig. 5.3B), It may be the case that high variation in background ratios, as well as high absolute values, prevented any signal from being detected in dung-receiving treatments in oil palm. High variation between oil palm seedlings could be due to heterogeneity in a number of unmeasured soil characteristics. For example pH, which is pivotal in the release of ammonia from soil, and could affect the natural $^{14}NH_4$: $^{15}NH_4$ in the rhizosphere prior to any treatment set-up. Previous studies indicate there are no differences in pH between vertical layers (Yavitt *et al.* 2009), however less is known about horizontal heterogeneity. Moreover, a declining baseline was observed in palm seedlings across the duration of the experiment, which could indicate that any potentially detectable incorporation was neutralized. The observed decline in baseline values may have resulted from some environmental influence, *i.e.* altering plant or soil stoichiometry. It may be that in oil palm I missed a peak in the assimilation of ^{15}N between the last two sample days (D_{65} and D_{233}). A delayed signal in oil palm compared to logged forest could occur for a number of reasons, including (i) altered nutrient dynamics in oil palm soils arising from removal of crop biomass, *i.e.* reduced nutrient returns, and addition of fertilisers, or (ii) the substantially larger size of the oil palm seedling compared to the dipterocarp seedlings. As I was not able to capture differences between dung-receiving treatments over time in the oil palm ecosystem I limit the rest of my discussion to the logged forest.

The absence of a non-labelled dung control treatment means I cannot precisely quantify uptake of DDN, as some of the assimilated ^{15}N in the dung-receiving treatments could have derived from ^{15}N-enrichment of the soil not associated with the ^{15}N tracer. An increase in the availability of ^{15}N in the soil could result from an enriched ammonium pool due to preferential uptake of $^{14}NH_4$ by microbes, combined with increased microbial biomass and activity in the presence of a rich energy source, dung. It would be interesting to explore further the different sources of nitrogen contributing to an increase in ^{15}N

assimilation over time. However, for the purposes of the discussion I refer to assimilated ^{15}N as DDN.

Short- versus long-term availability of dung-derived nitrogen (DDN)

In logged forest the assimilation of ^{15}N by seedlings exposed to dung-receiving treatments began to deviate from the *soil only control* at approximately 20 days. Based on observations within one month from a similar study conducted in temperate pastures (Nervo *et al.* 2017), and an expectation that processes are accelerated in tropical soils, I had anticipated that assimilation of DDN by aboveground biomass would peak earlier. Tropical forests have been shown to have faster transfer of faeces into the soil (Slade *et al.* 2007), faster turnover of plant tissue (Gill & Jackson 2000) and forest biomass (Stephenson & Van Mantgem 2005), and lower forest floor nutrient residence time (Foster & Bhatti 2006) compared with temperate forests. Moreover, ^{15}N assimilation did not plateau over the 8-month duration of the experiment, suggesting that the nitrogen is more strongly locked into the dung than I expected despite the efficient nutrient cycling in the tropics (Swift *et al.* 1998). The leaf samples I collected after 21 months remained enriched compared to the baseline value at $D_{0,}$ but there was no longer any difference among dung-receiving treatments. I can therefore assume that either DDN was potentially still available for assimilation by plants, or nitrogen had not fully turned over in the plant tissue.

There was early detection of DDN in the soils, especially in the presence of dung beetles (Fig. 5.4). Dilution of DDN from endogenous nitrogen in the soil (Clough *et al.* 2013) could explain the absence of treatment effects in foliar samples in the short term, owing to a slower accumulation of ^{15}N in seedling tissues. This may be more pronounced in tropical than temperate systems, as nitrogen pool sizes, and rates of production of plant-available nitrogen, are higher in many tropical forest soils compared to temperate soils

(Pajares & Bohannan 2016), possibly due to higher relative abundance of nitrogen-fixing leguminous trees (Vitousek 1984).

Dung beetle presence appears to reduce nitrogen availability to plants

In the presence of dung there was high levels of DDN incorporation into the soil from the very first days, as indicated by the high intercept, and levels remained high for the duration of sampling. In the absence of dung beetles DDN content increased over time, but only reached similar levels to soils with dung beetle present after approximately 50 days. However, contrary to our predictions, in logged forest dung beetle presence decreased the assimilation of DDN into the aboveground biomass of seedlings over time. Although I did not examine changes to the different nitrogen pools over time, I interpret this result given the current literature on nutrient cycling and linked biological processes, and the potential effects of dung beetle presence and absence.

I expected that dung beetle presence would increase assimilation of DDN as previous work suggests that dung beetle activity accelerates bacteria-mediated nitrogen mineralization rates by increasing carbon and nitrogen levels in the upper soil layers, facilitating bacterial growth (Yokoyama *et al.* 1991). However, a full account of the effect of dung beetle activity on nitrogen flows and distributions has not been conducted, and the benefits of increased nitrogen mineralization could be offset or even outweighed by activities which decrease the availability of nitrogen to plants (Nichols *et al.* 2008). One such example would be denitrification (the pathway through which NO_3^- or NO_2^- are sequentially reduced to N_2) in brood balls causing a N loss significantly greater than that from un-manipulated dung (Yokoyama *et al.* 1991).

Alternatively, burial of dung by tunnellers may remove dung, and products of its mineralisation, from the rhizosphere of the seedlings, thereby delaying uptake until sufficient root growth and mycorrhiza colonisation allow access to the buried dung. Thus, given the ephemeral nature of mammalian dung, it is feasible that its burial acts as an advantageous ‘storage’ of nutrients for later usage by aboveground biomass. Delayed transfer of the dung through the soil profile in the absence of dung beetles points to transfer (i) by smaller organisms, (ii) via a chain of biotic links, or (iii) by abiotic processes, such as rainfall and leaching. Contrary to expectation, soil ^{15}N was not related to the depth of the soil sample. However, I see evidence of DDN moving through the soil column, with maximum enrichment in the most superficial layer at D_4 followed by a sharp decline, and then fairly constant enrichment at middle depths up until D_{14}, and evidence of enrichment across the period up until D_{64} in the deepest layer (see supplementary Figs. 5.9 and 5.10). This would align with our expectation of a depth effect on soil enrichment due to the activity of larger beetles moving dung to lower soil levels over time, and gradual leaching of nutrients with rainfall. There was an interactive effect between treatment and distance to the nearest mature tree upon the amount of DDN incorporated into the soil. This could be the result of beetle activity changing the availability for uptake by the root networks of proximal large trees, and thus the residual pool. However, the mechanisms may be more complicated, including the relationship between dung beetles and root-associated fauna.

Lower assimilation rates by seedlings in the dung beetle treatment could be due to dilution of the dung-derived ^{15}N. Our new method of dung labelling through administration of the ^{15}N label to cattle drinking water (*i.e.* the forage fed to the cattle was not ^{15}N-labelled) only labelled the faecal endogenous nitrogen component (excreted microbes). It is possible that mineralisation of labelled and biologically distinct non-labelled components of the dung were affected to different degrees under dung beetle presence. An increase in mineralisation of non-labelled components, and a corresponding increase in background nitrogen pools, would lead to increased dilution of dung-derived ^{15}N, and therefore a lower assimilation rate by seedlings. Acceleration of natural nitrogen mineralization processes could be attributed to dung-beetle mediated enhancement of the *priming effect*, defined as the removal of energy limitation for microbial growth by the input of an easily decomposable energy source (Kuzyakov *et al.* 2000). Given that microbial biomass increases with the complexity of meso- and macrofaunal communities (Vedder *et al.* 1996), I postulate that the complex trophic interactions inherent to tropical food webs (Barnes *et al.* 2017) should result in relatively high microbial biomass. The latter exposed to dung-beetle elevated priming, could have led to increased microbe-mediated nitrogen mineralisation, and therefore dilution of labelled nitrogen. Unfortunately, I still have a very limited understanding of how dung burying and bioturbation activities affect soil microbial and faunal biomass, community composition, and complexity.

While this method led to some heterogeneity of dung labelling, this drawback was outweighed by true incorporation of the ^{15}N label into the dung matrix compared to previous methods (Nervo *et al.* 2017) which incubate dung organic matter with the dissolved ^{15}N-compound. For example, one month of total NH_4^+ and NO_3^- availability in the first soil layer (0-5 cm) was enhanced by dung beetle presence in Alpine pasture (Nervo *et al.* 2017). The authors hypothesised that transport of dung material along the soil profile may be accompanied by microbially-driven mineralisation of exogenous organic nitrogen and release of dung-derived NH_4^+. However, NH_4^+ and NO_3^- availability in the superficial soil layers may be unrealistically inflated by highly mobile labelled N compounds which are not truly incorporated into the dung matrix. This inflation would be of particular concern in tropical ecosystems with high rainfall.

Future directions

Further studies should investigate how dung beetles interact with less well-studied components of the decomposer food web, *i.e.* micro-fauna and mesofauna, and microbes and fungi. The N cycle is regulated by soil organisms with particularly high functional specificity compared to other nutrient cycles (Swift *et al.* 1998), which heightens the importance of revealing such above- and belowground interactions. Furthermore, I increasingly understand that conversion of natural habitat to agricultural use alters the community of soil flora and fauna (Tscharntke *et al.* 2012). Given the increasing cultivation of oil palm in tropical regions (Fitzherbert *et al.* 2008), there is a pressing need to understand the implications of conversion from forest to planation for nutrient cycling, and other associated ecosystem functions.

Supplementary Methodology (Chapter 5)

S5.1. Dung processing

Logged forest: A total of 3.07 kg of ^{15}N—labelled dung was collected. This was homogenized by hand and 610 ml of rainwater was added in order to moisten the dung. Total weight was increased to 3.70 kg, from which 0.12 kg of wet weight dung was taken for analysis on the mass spectrometer. The remaining 3.58 kg was divided into 12 pats of ~15 cm diameter each weighing 300 g ± 8 g (SD 2.27).

Oil palm: A total of 5.19 kg of ^{15}N—labelled dung was collected. This was homogenized by hand. Moisture level was considered sufficient for dung beetle removal so water was not added. 0.12 kg wet weight of dung was taken for analysis on the mass spectrometer. The remaining 5.07 kg was divided in 12 pats of ~15 cm diameter each weighing 410 g (SD 2.04). Dung was kept refrigerated for 72 hours before being added to the mesocosms.

S5.2. Soil $\delta^{15}N$ data processing

Although the elemental nitrogen content of many samples fell below the threshold for stable $\delta^{15}N$ values (Fig. S5.4), there was no significant relationship between $\delta^{15}N$ and µg elemental nitrogen (Fig. S5.5). Furthermore, I looked at variability of $\delta^{15}N$ for each discrete experimental day (Fig. S5.6) in order to ensure that variability (*i.e.* variable drift away from true values) was altered across the duration of the experiment.

S5.3. Accuracy of isotopic measurements

In order to assess accuracy of isotopic measurements on leaf and soil material, I calculated the mean and standard deviation of isotopic measurements on casein IRMS standard.

Material	caesin mean	caesin SD	n
Leaves	6.744	1.033	36
soil	5.928	0.435	47

Supplementary Tables (Chapter 5)

Table S5.1. Water volume and concentration of ^{15}N-ammonium consumed by cattle over the period of 43 h after administration in both ecosystems. N.B. for logged forest one of two the drinking pails was destroyed between T_0 and T_{24HR} (cattle were never water limited).

Ecosystem	*Time period* *(0 =administration)*	*Average concentration* *^{15}N-ammonium (µg /L)*	*Water volume* *consumed by cattle (L)*	*Average concentration* *^{15}N-ammonium (µM)*
Logged forest	**0-24**	**10824**	**6 + unknown amount (spillage)**	**600**
Logged forest	**24-43**	**3042**	**14**	**168.6**
Oil Palm	**0-24**	**10824**	**20**	**600**
Oil Palm	**24-43**	**6247**	**15**	**346.3**

Table S5.2. Number of individuals of each species of dung beetle added to the dung + beetle treatments.

Species	No. individuals added to each mesocosm
Oil palm	
Catharsius rendaupauliana	6
Onthophagus cervicapra	3
Onthophagus obscurior	10
Proagaderus wantanabei	3
Logged forest	
Catharsius dayacus	2
Catharsius rendaupauliana	5
Copris sinicus	2
Microcopris doriae	2
Onthophagus cervicapra	3
Onthophagus obscurior	24
Onthophagus rugicollis	24
Onthophagus vulpes	2

Table S5.3. Model comparison for optimization of the random and fixed components sequentially of the generalized lest squares (GLS) model for logged forest leaf data. AIC column gives the Akaike information criterion (AIC) model fit given the full dataset. Black lines represent the best models, and the emboldened values highlight the when the model fit was improved compared to the previous best structure.

Model structure	**Parameter estimation**	**AIC**
Random component		
corCAR1 (form = ~ 1 | Mesocosm)	REML	-3125.72
corCAR1 (form = ~ 1 + Day | Mesocosm)	REML	**-3211.17**
corCAR1 (form = ~ 1 + Day | Mesocosm), weights =varIdent (form = ~ 1 | Treatment)	REML	-3195.34
corCAR1 (form = ~ 1 + Day | Mesocosm), weights =varIdent (form = ~ Day)	REML	**-3250.10**
Fixed component		
^{15}N ~DistMature + Treatment + Day + Treatment:Day + DistMature:Treatment + DistMature:Day +DistMature:Treatment:Day	ML	-3753.14
^{15}N ~DistMature + Treatment + Day + Treatment:Day + DistMature:Treatment + DistMature:Day	**ML**	**-3736.55**
^{15}N ~DistMature + Treatment + Day + Treatment:Day + DistMature:Treatment	**ML**	**-3738.45**
^{15}N ~DistMature + Treatment + Day + Treatment:Day	**ML**	**-3742.25**
^{15}N ~DistMature + Treatment + Day	ML	-3721.33
^{15}N ~ Treatment + Day + Treatment:Day	ML	-3744.16

Table S5.4. Model comparison for optimization of the random and fixed components sequentially of the generalized lest squares (GLS) model for oil palm leaf data. AIC column gives the Akaike information criterion (AIC) model fit given the full dataset. The emboldened values highlight the when the model fit was improved compared to the previous best structure.

Model structure	**Parameter estimation**	**AIC**
Random component		
corCAR1 (form = ~ 1 | Mesocosm)	REML	-3293.8
corCAR1 (form = ~ 1 + Day | Mesocosm)	REML	-3293.8
Fixed component		
^{15}N ~DistMature + Treatment + Day + Treatment:Day + DistMature:Treatment + DistMature:Day +DistMature:Treatment:Day	ML	-3772.27
^{15}N ~DistMature + Treatment + Day + Treatment:Day + DistMature:Treatment + DistMature:Day	**ML**	**-3775.76**
^{15}N ~DistMature + Treatment + Day + Treatment:Day + DistMature:Treatment	**ML**	**-3776.82**
^{15}N ~DistMature + Treatment + Day + Treatment:Day	**ML**	**-3780.17**
^{15}N ~DistMature + Treatment + Day	ML	**-3753.24**
^{15}N ~ Treatment + Day + Treatment:Day	ML	-3781.90

Table S5.5. Model comparison for optimization of the random and fixed components sequentially of the generalized lest squares (GLS) model for logged forest soil data. AIC column gives the Akaike information criterion model fit given the full dataset. The emboldened values highlight when the model fit was improved compared to the previous best structure, *i.e*. lower AIC.

Model structure	**Parameter estimation**	**AIC**
Random component		
corCAR1 (form = ~ 1 | Mesocosm/Depth)	REML	-8117.6
corCAR1 (form = ~ 1 + Day | Mesocosm/Depth)	REML	**-8120.4**
Fixed component		
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Depth:DistMature + Treatment:DistMature + Day:DistMature + Depth:Treatment:Day + Depth:Treatment:DistMature + Depth:Day:DistMature + Treatment:Day:DistMature	ML	-9500.9
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Depth:DistMature + Treatment:DistMature + Day:DistMature + Depth:Treatment:Day + Depth:Treatment:DistMature + Depth:Day:DistMature	**ML**	**-9504.5**
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Depth:DistMature + Treatment:DistMature + Day:DistMature + Depth:Treatment:Day + Depth:Treatment:DistMature	**ML**	**-9508.1**
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Depth:DistMature + Treatment:DistMature + Day:DistMature + Depth:Treatment:Day	**ML**	**-9515.7**
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Depth:DistMature + Treatment:DistMature + Day:DistMature	**ML**	**-9518.2**
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Depth:DistMature + Treatment:DistMature	**ML**	**-9520.2**

15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Depth:DistMature	ML	-9512.1
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:Day + Treatment:DistMature	ML	**-9523.1**
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Depth:Day + Treatment:DistMature	ML	-9519.7
15N ~ Depth + Treatment + Day + DistMature + Depth:Treatment + Treatment:Day + Treatment:DistMature	ML	-9523.2
15N ~ Depth + Treatment + Day + DistMature + Treatment:Day + Treatment:DistMature	**ML**	**-9526.8**
15N ~ Treatment + Day + DistMature + Treatment:Day + Treatment:DistMature	ML	-9530.1

Supplementary Figures (Chapter 5)

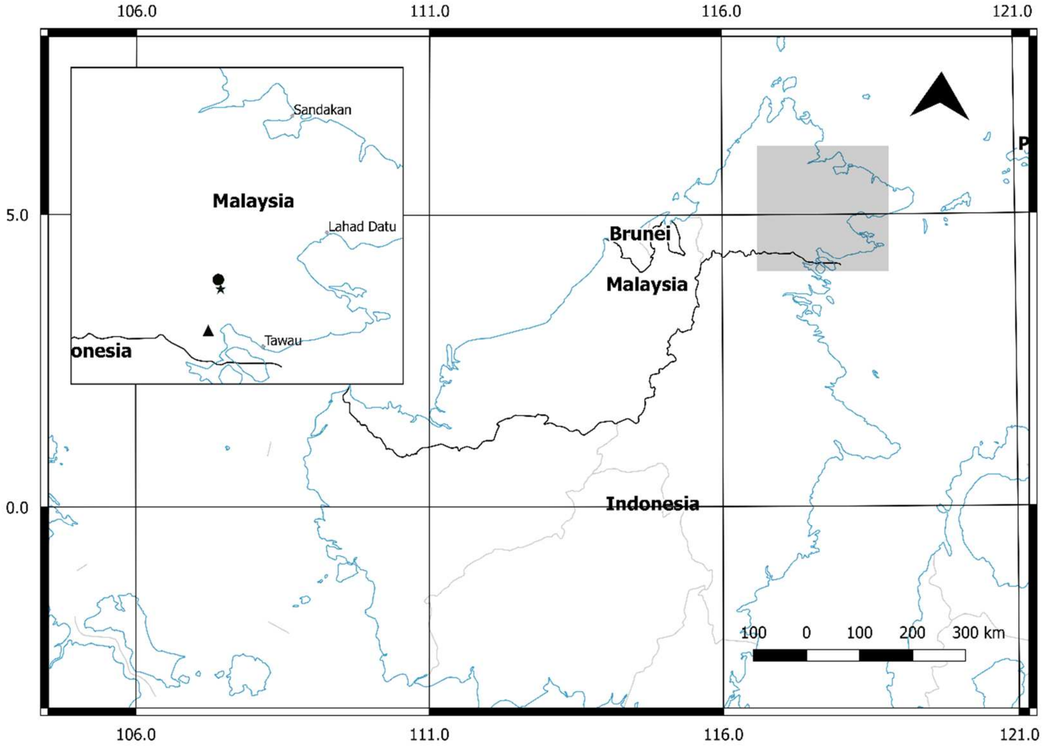
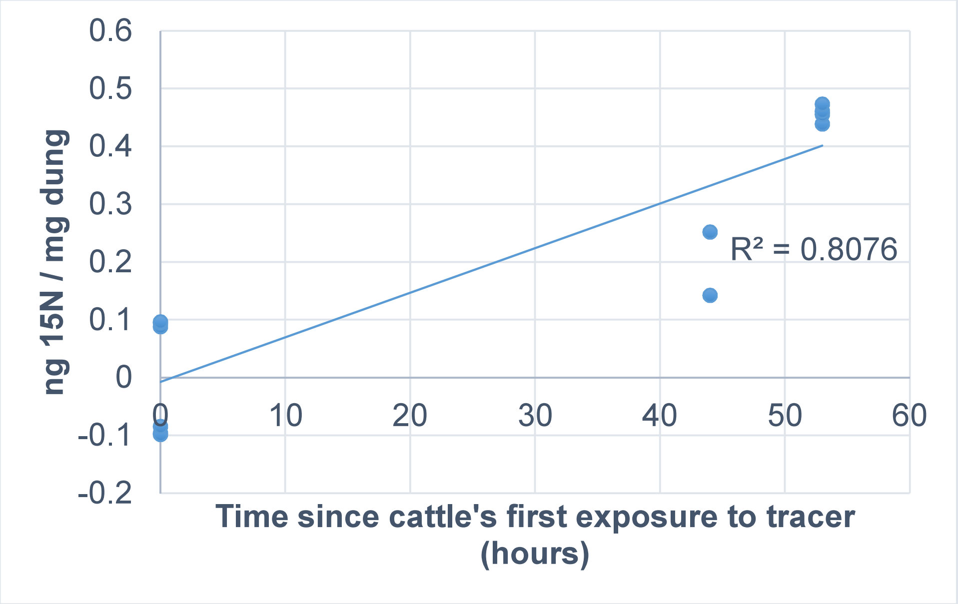


Fig S5.1. A map of the two field sites (circle = logged forest; star = oil palm), and local farm used to produce labelled dung (triangle). The forest site is continuous twice-logged lowland dipterocarp forest located inside the Stability of Altered Forest Ecosystems (SAFE) project, a 7200 ha experimental landscape. The oil palm site is continuous oil palm within the Menggaris Estate, located approximately 17 km from the SAFE project site.



[B]

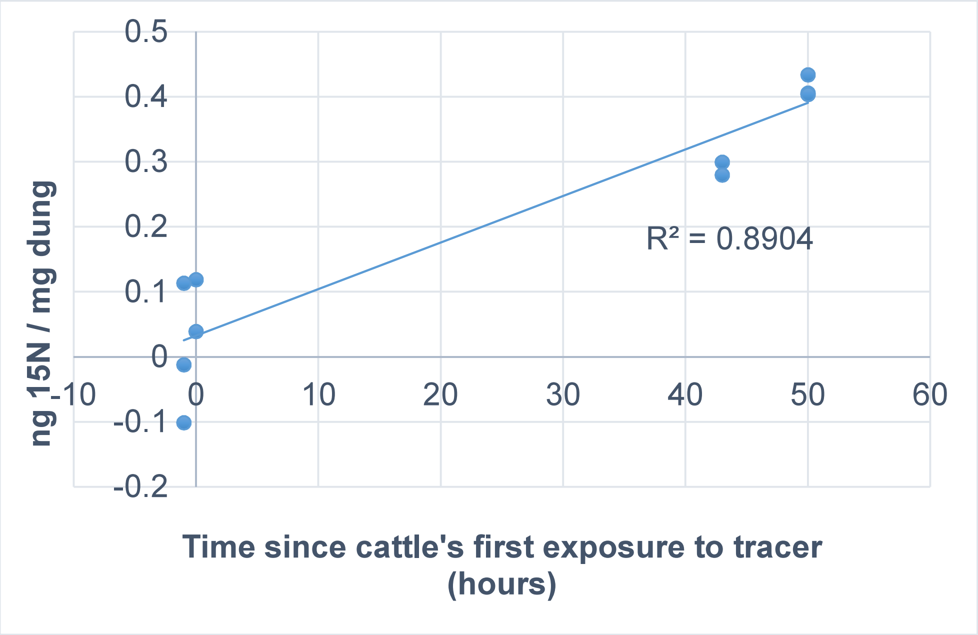


Figure S5.2. Enrichment of cattle dung over time reported in ng ^{15}N/ mg dung. At T_0 cattle were presented with a single water source of 600 μM solution of ^{15}N-ammonium. Graphs show the timeline of dung enrichment for the dung used in the two ecosystem types [A] logged forest, and [B] oil palm plantation.

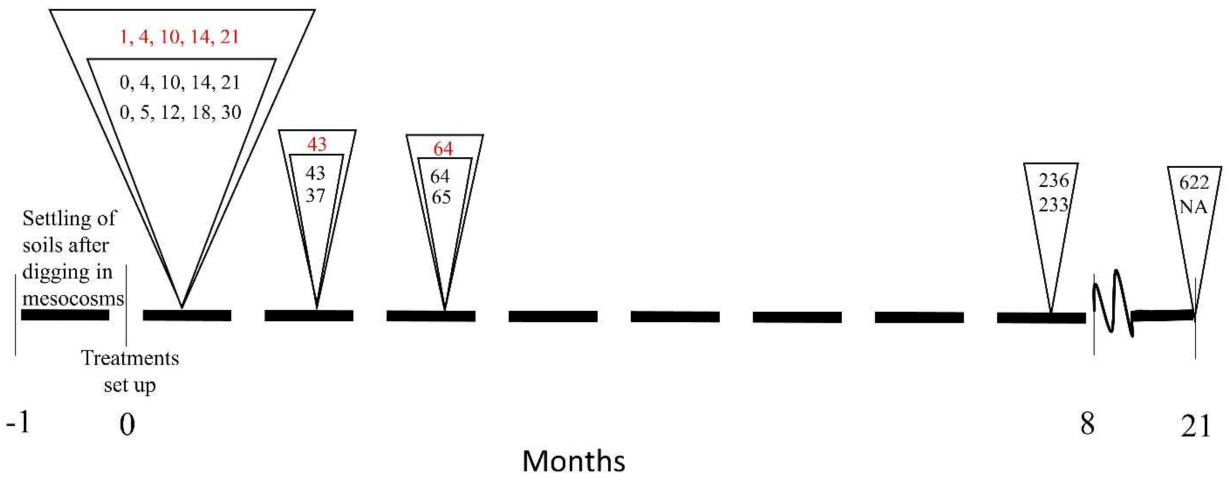


Figure S5.3. Timeline of the experiment over 8 months, where 0 is the beginning of the experiment, as defined by the planting of the dipterocarp and palm seedlings. The timeline begins at (-1) in order to show the preparation prior to the beginning of the experiment. The red numbers inside the larger triangles are the days on which soil samples were taken from logged forest. The black numbers inside the lower triangles are the days on which leaf samples were taken from [upper line of numbers] logged forest and [lower line of numbers] oil palm.

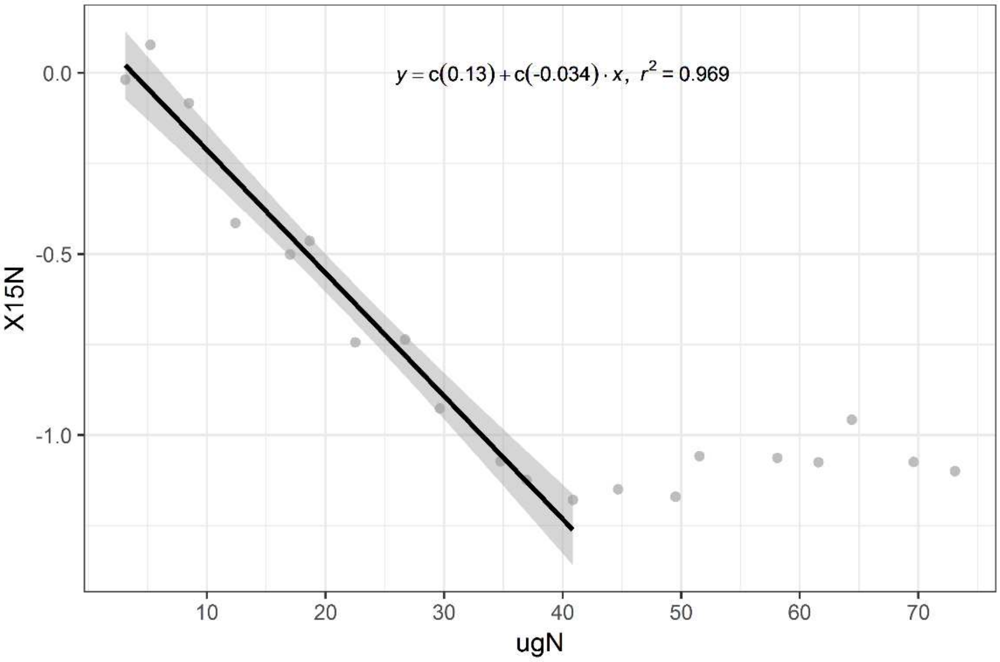


Figure S5.4. Soil δ^{15}N plotted against nitrogen elemental weight. The regression line is fitted only through observations with nitrogen elemental weight < 40 µg in order to highlight the relationship drift away from the true δ^{15}N value. The equation of the regression line is inlaid.

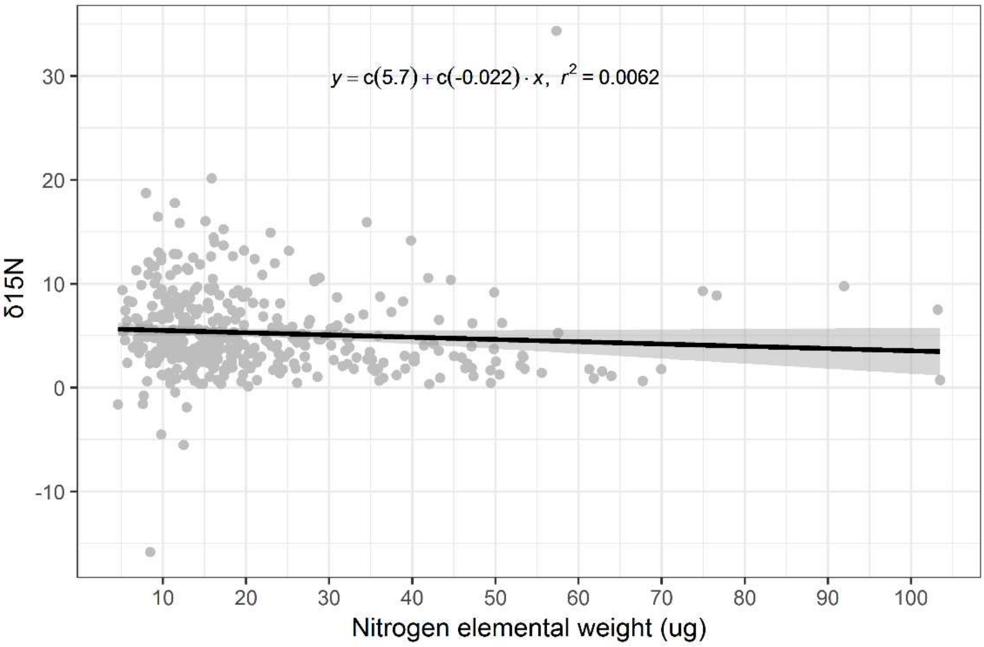


Figure S5.5. Soil δ^{15}N plotted against nitrogen elemental weight. Points represent the full, unfiltered dataset of soil samples (n = 377), and the black line is the equation of the linear model for soil δ^{15}N by the elemental weight of nitrogen (µg). The grey area represents SE around the modelled relationship.

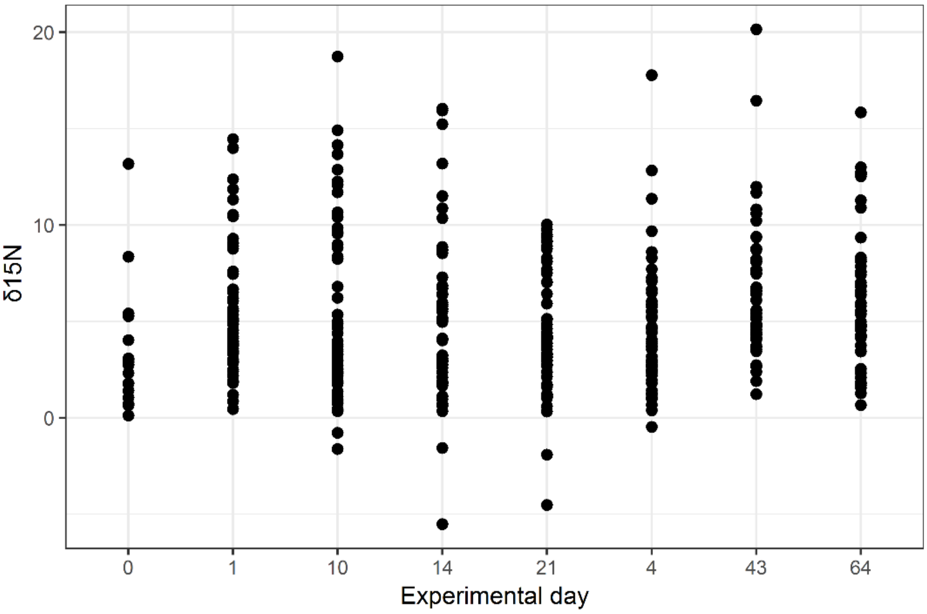


Figure S56. Soil $\delta^{15}N$ plotted against experimental day. Points represent the full, unfiltered dataset of soil samples (n = 395). Here, treating experimental day as a categorical variable, I observe that the variation in $\delta^{15}N$ is similar across the duration of the experiment.

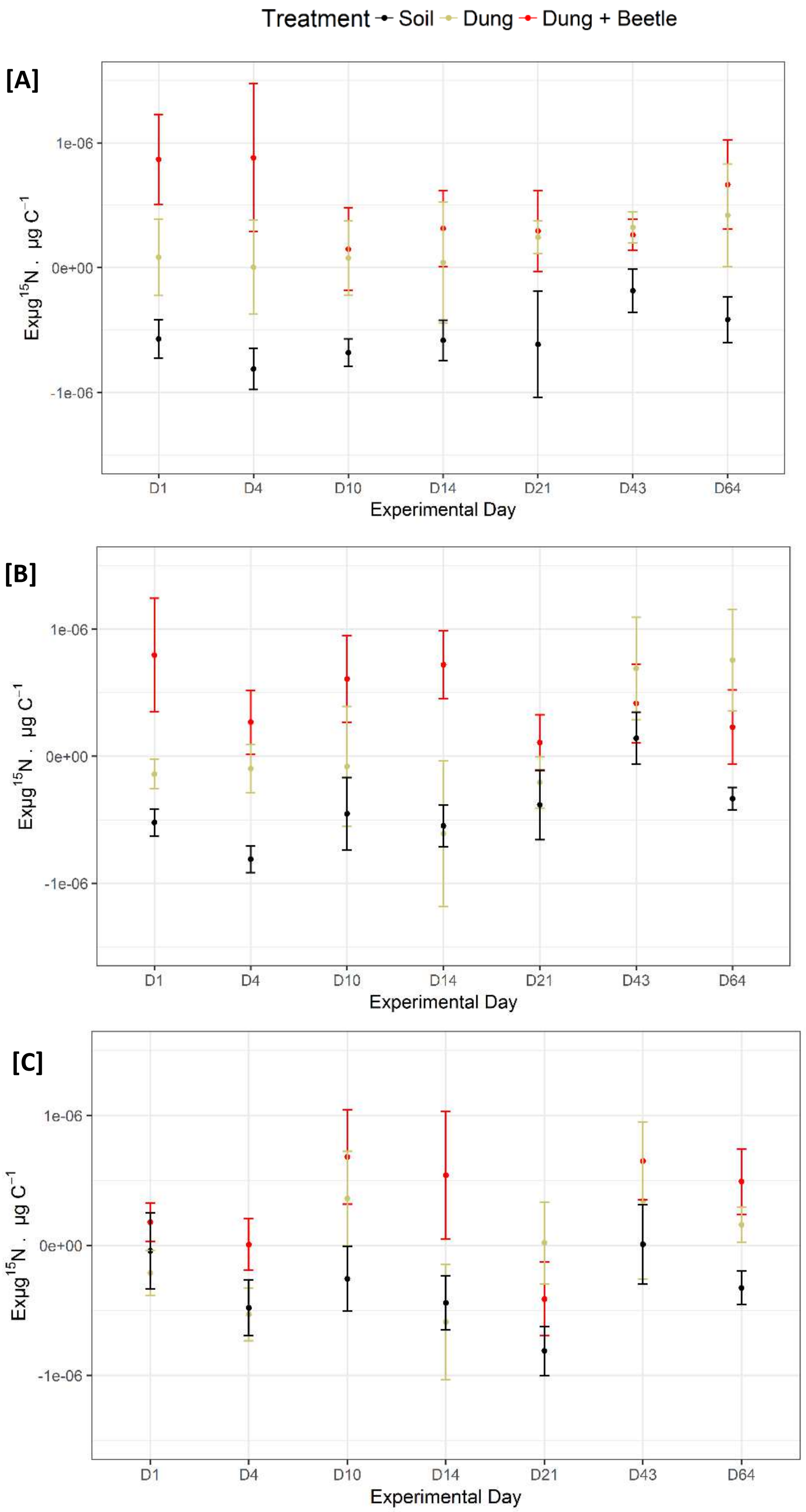


Figure S5.7. Mean ± SE assimilated ^{15}N of logged forest soil samples over the experimental period. Observations are coloured by treatment, where black = *soil only control*, yellow = *dung only*, and red = *dung + dung beetle*s.

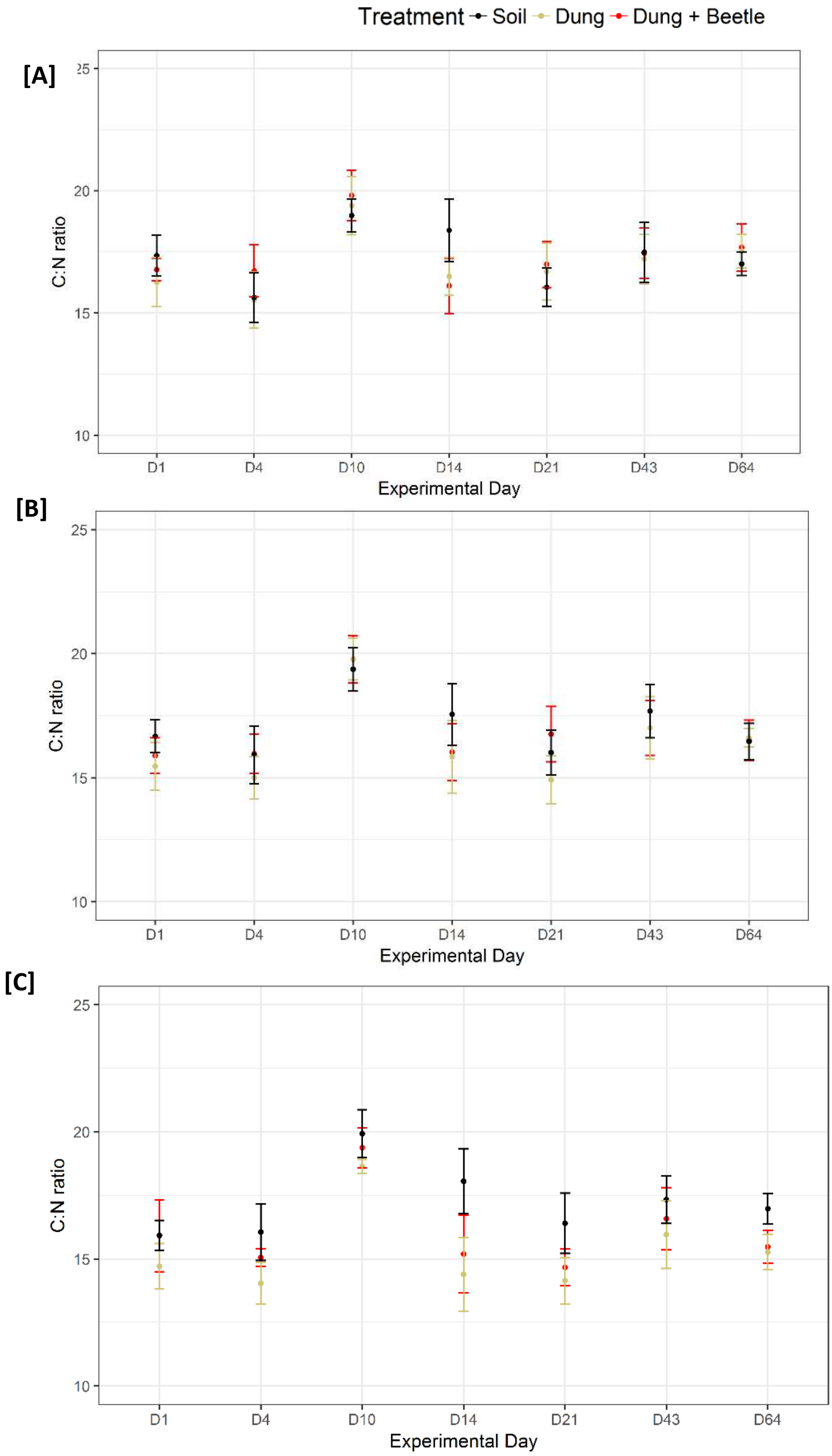


Figure S5.8. Mean ± SE C: N ratio of logged forest soil samples over the experimental period. Observations are coloured by treatment, where black = *soil only control*, yellow = *dung only*, and red = *dung + dung beetles*.

CHAPTER 6

General conclusions

Crocker Range, Sabah

Main findings

The overarching aim of this research was to increase our understanding of altered ecosystem functioning in human modified tropical landscapes, with a focus on logged forests and oil palm plantations. I used stable isotope analyses of carbon and nitrogen to explore how anthropogenic modification re-directs the pathways of energy and nutrient flows through ecosystems, with potential consequences for ecosystem resilience and the capacity for provisioning services, *e.g.* soil fertilisation and biocontrol. In exploring the effects of logging I focused on changes to the resource use and functional role of insectivorous bat populations and communities. To understand the link between biodiversity and decomposition processes I focused on dung beetles, a specialist component of the soil macrofauna, and their role in nitrogen recapture by aboveground biomass. The analyses conducted lead me to present the following major conclusions:

Bat assemblages differ over a broad gradient of degradation

Few studies have investigated the response of bat populations and communities to the impacts of logging in the Paleotropics, with far more focus on their Neotropic counterparts (Meyer *et al.* 2015). In chapter 2, I analysed a four-year dataset to investigate the impact of different logging histories upon Paleotropic assemblages in terms of community diversity, taxonomic composition and total abundance. Furthermore, I investigated interannual changes to community metrics in response to emergent stressors in the environment, *e.g.* active logging and severe, short-term drought. In logged forest sites, compared to unlogged, there were very weak effects on species richness, but pronounced decreases in total abundance and changes in community composition, *i.e.* relative abundance of species. Community metrics were more consistently and severely affected over space than time, supporting the widely held view that logging effects upon biodiversity can persist over long time scales (Ewers & Didham 2014). Although I did not investigate synergistic effects of long-term logging impacts and short-term climatic changes, the findings add weight to the need to consider multiple pressures in concert to protect the biodiversity of terrestrial tropical landscapes.

I conducted this analysis in such a way as to enable among-site comparisons, providing the context for the analyses in chapters 3 and 4. This work could be developed further by aligning assemblages along a gradient of forest-structure metrics, making the outcomes useful for predicting future changes to bat communities under different forest management strategies (Struebig *et al.* 2013). In subsequent chapters 3 and 4, I assessed the shifts in resource use at the population level, *i.e.* individual bat species, and did this cautiously given that changes to the resource use and functional role of abundant bat species are potentially sensitive to changes in the abundance of other bat species. *e.g.* relief from niche partitioning (Broders *et al.* 2014; Roswag *et al.* 2015). In chapter 3, I conducted community analyses over a narrower gradient of degradation (*i.e.* only within regenerating forest), to refine the community context for the observed changes in niche breadth and trophic position.

Habitat quality thresholds: ecosystem function versus classic community metrics

In chapter 3 I examined the response of trophic interactions, and associated energy fluxes, across a relatively narrow gradient of logging intensity. Focusing on insectivorous bats, I applied stable isotope analyses to assess how consumer resource use varied with habitat quality. This chapter brought novel insights to the conservation value of secondary forest, highlighting the importance of considering both local disturbance history and landscape context. The study supports recent evidence that habitat quantity thresholds for healthy ecosystems are higher than previously considered, owing to prior focus on classic community metrics (De Coster *et al.* 2015). There are few studies which have quantified the trophic position and niche breadth for mobile higher-level predators, and those papers often do not use landscape-scale data, rather focusing on inter-population differences at a particular location. I overcame previous limitations by combining newly-developed analyses of stable isotope data with intense sampling of bats across a large-scale experimental landscape, where environmental gradients are well described by both ground-based and remote-sensed methods. Recent research is concerned with ecological interactions between species, how they may be perturbed by anthropogenic activities, and the consequences for ecosystem functions and services (Barnes *et al.* 2017). My findings bring new and interesting insights into the effects of habitat modification on trophic complexity and food chain length, and suggest that functionally-important shifts may be uncoupled from shifts in predator composition. The management of habitat embedded within matrix landscapes is highly topical, especially in the tropics given high rates of land-use change (Ewers *et al.* 2011). My findings can help develop a clear conceptual basis for the practical assessment of habitat value, and thereby facilitate regional and national conservation targets.

Food web structure differs over a broad gradient of degradation

In chapter 4 I built upon the findings from chapter 3 to investigate changes in food web structure over a wider gradient of human disturbance from primary to repeatedly-logged forest, utilising a highly resolved axis of forest-structure derived from remote-sensed data. Moreover, I explored temporal, spatial and interactive effects upon the response of whole communities. Shifts in resource use by mobile, generalist predators can decrease the asymmetry and stability of food webs (McCann *et al.* 2005; Rooney *et al.* 2006; Bartley *et al.* 2018), but remain challenging to resolve. Using stable isotope techniques I found that bat populations differed in ^{13}C-enrichment across the spatial gradient, potentially due to increased dependence on the detrital food web compartment (Wolkovich *et al.* 2014; Perkins *et al.* 2018). Furthermore, I found stronger interannual effects than expected, and interactive effects of long- and short-term environmental changes. Changes in isotopic values of predator populations over time were of a similar direction and magnitude to spatial changes, hinting at a potentially impactful synergy between local pressures and global climatic pressures upon food web stability. In chapter 4 I found that species' isotopic niche did not vary across the gradient of logging impact, in contrast to the pronounced change over a much narrower gradient of disturbance in chapter 3. This disparity likely reflects the sensitivity of niche parameters to different biotic and abiotic processes. The niche concept is a very powerful tool for predicting ecological responses to environmental stressors (Holt 2009), however there are still major challenges in the interpretation of the response.

Insectivorous bats have recently been shown to derive their energy from a combination of the green and the brown food chain (Hyodo *et al.* 2010), similarly to many predators occupying high trophic levels (Wolkovich *et al.* 2014). I intended to explicitly investigate shifts to the dependence of insectivorous bat populations and assemblages upon green and brown resources associated with habitat degradation. However, major resources representing these energy channels, *i.e.* fresh leaves and leaf litter, were not sufficiently distinct in their isotopic composition to allow analysis of relative contribution via mixing models (Phillips *et al.* 2014). Recent interesting work observed both density-dependent and density-independent consumption of green resources among functional groups in other generalist predators (Perkins *et al.* 2018), suggesting differential sensitivities to biotic and abiotic changes associated with habitat modification. Future work in the tropics could take advantage of radioisotopes of carbon in order to facilitate detection of shifts between basal resources which are similar in terms of natural abundance stable isotope ratios of carbon (Haraguchi *et al.* 2013).

Biodiversity affects decomposition processes

Chapter 5 improves our understanding of the role of soil mesofauna in decomposition processes in tropical soils. My development of novel methods of isotope-tracer addition to soil systems and use of a model taxon with increasingly well-resolved ecology, provided a powerful pathway for studying the link between biodiversity and ecosystem functioning. I showed that the presence or absence of dung beetles had an effect upon the rate at which dung-derived nitrogen was incorporated into the soil, and assimilated by aboveground primary producers. My results suggest that both rate and maximal recapture of nitrogen by producers may be affected by dung beetle presence, but study beyond the eight-month duration of my experiment would be required to conclude the latter decisively. My results are contrary to predictions from previous studies and current understanding of the effects of dung beetles on nitrogen cycling, having shown a negative relationship between dung beetle presence and the rate of nitrogen assimilation. Thus, I highlight the importance of further work to improve our understanding of above- and below-ground interactions and associated ecosystem functions. This study delivered a new method for dung labelling, both affordable and sufficient to trace through multiple dilution pools, highlighting its potential ecological application to address emerging challenges in natural and human-dominated systems.

Limitations and future directions

Methodological constraints in the study of logging effects

There remains much inconsistency in the response of tropical biodiversity to logging (Newbold *et al.* 2014; Thorn *et al.* 2018). While a significant factor is the distinct responses of different taxa, an additional contributor is comparison among logging-effect studies using varied methods of impact classification. For example, logging history of an area can vary by intensity of timber removal, spatial extent into surrounding land, and frequency over time, with implications for ecological response (Malhi *et al.* 2014). The complexity of classification has recently prompted the study of ecological responses along disturbance gradients, including forest-structure characteristics (Struebig *et al.* 2013), facilitated by increased availability of reliable remote-sensed data (Jucker *et al.* 2018b). In this work, I was able to take advantage of high resolution LiDAR data characterising all sample sites, moving away from the constraints associated with conventional discrete classification of sites. In either case, there remain methodological constraints inherent in the widely applied spatial comparisons of logged versus unlogged forest treatments. Natural environmental variation between sites, and associated changes to ecological processes, can affect interpretation of biodiversity response to treatment effects (Hamer *et al.* 2003; Gardner *et al.* 2009). Sites in this study were located in such a way as to minimise environmental variation, *i.e.* accounting for altitude and slope (Ewers *et al.* 2011), however increased replication would further minimise the potential for logging effects to be obscured by natural variation.

Spatial scale of the study

Spatial autocorrelation is a general property of ecological variables observed across gradients (Legendre 2012), and it has received research attention in tropical forest ecosystems (Morlon et al. 2008). Spatial autocorrelation reflects how the focal variable (*e.g.* species composition) at any given location is influenced by surrounding locations. In chapter 3, I cautiously increased replication by conducting analysis at the level of the vegetation plot, and did not detect any effects of spatial autocorrelation for the single-year dataset. The average home range of understorey insectivorous bats, at 44Ha, is 4-15 times smaller than that of larger forest mammals (Struebig *et al.* 2013). Thus, when focusing on resource-use, localities which are closer together may be considered independent for bats but possibly not for other larger mammals.

Access to high-resolution LiDAR data allowed populations and communities, and associated ecological parameters, to be aligned along meaningful axes of forest structure. Furthermore, habitat characterisation was possible at any spatial scale given availability to data over the full 72 000Ha extent of the SAFE project. This high degree of flexibility presented the challenge of determining the most relevant spatial scale at which to characterise the habitat of bat assemblages. Specific to my research taxa, there exists relatively poor data regarding home ranges of different insectivorous bat species (Klingbeil & Willig 2010). Furthermore, there is strong evidence that guilds perceive different landscape characteristics at different spatial scales (Ducci *et al.* 2015), thus it would be interesting to test the effects of quantifying vegetation traits at a range of relevant scales. More generally, there is recent focus on the landscape context of remnant forest in terms of conservation value (Turner *et al.* 2012), and more scale-sensitive analyses could help inform landscape management. Indeed, a previous study shows that, for birds, proximity to forest patches is more important for habitat suitability than local vegetation structure (Singh *et al.* 2017). My work analysed the impacts of local and landscape scale habitat quality on ecosystem functioning, but explicit focus on the effects of spatial scale is a clear avenue for further research.

In chapter 4 I found a positive relationship of trophic position with forest vertical complexity, compared to the negative relationship with canopy height observed in chapter 3. The two chapters differed in the spatial scale at which populations were characterised, *i.e.* at the level of site and vegetation plot for chapters 3 and 4, respectively. Moreover, in chapter 3 canopy height was estimated as a point measure at the centroid of each plot, whereas in chapter 4 all habitat variables included in PC1 were estimated from 1 km polygons around site-level centroids. The method in chapter 3 characterizes the location in the vicinity of the harp traps, whereas the method in chapter 4 reveals information about the nearby forest. These differing scales need to be considered when interpreting these results and indeed any spatially-sensitive metrics.

Natural abundance stable isotope analyses

Natural abundance stable isotope investigations over the past three decades have focused on trophic characteristics for a wide variety of terrestrial taxa including bats, elephants, bears, chimpanzees and hummingbirds (Fry 2008; Broders *et al.* 2014). However, application to the study of ecological and behavioural characteristics remains underused (Crawford *et al.* 2008), and will likely increase with greater understanding of metabolic effects upon isotopic behaviour, and development of less simplified dietary indices (*e.g.* trophic position; Martinez del Rio *et al.* 2009); advancement of techniques focusing on specific compounds within tissues as opposed to bulk analyses (Ramos & González-Solís 2012); and use of multiple diet tracing methods in compliment (Nielsen *et al.* 2018). More empirical data underpinning methods for data processing (*e.g.* application of trophic enrichment factors, lipid standardisation or correction against spatial or temporal isotopic baselines) is required for terrestrial ecosystems given that models are often highly biased towards aquatic systems (Vanderklift & Ponsard 2003; Kiljunen *et al.* 2006).

Baseline correction of consumer $\delta^{15}N$ values is widely applied in natural abundance isotope studies. Site differences in $\delta^{15}N$ are more common than $\delta^{13}C$ due to large intra-system variation in nitrogen inputs, in the form of anthropogenic pollution (Korobushkin et al. 2014) and due to differential BGC cycling, *i.e.* nitrogen acquisitions from geological sources (Craine *et al.* 2015). Site-specific $\delta^{15}N$ has been recognised as a source of bias in studies comparing sites unless a 'local' baseline is used (Woodcock *et al.* 2012), with differences evident at a spatial scale of <1 km (Ponsard & Arditi 2000). This is a general rule, but is also an area of study in the context of modified landscapes, where among-site differences in baseline $\delta^{15}N$ may arise from changes in microbial activity, selective nitrogen loss of non-plant-available forms of inorganic nitrogen via compaction, erosion or leaching, and reduced input from leaf litter and rotting wood (Craine *et al.* 2015). Heterogeneity in $\delta^{15}N$ values as a result of habitat modification can be accompanied by substantial among-site variation in baseline $\delta^{13}C$ values, which to date appears to be overlooked. For example, the changes in microclimate associated with forest gaps could lead to ^{13}C-enriched baselines (Kohn 2010; Jucker *et al.* 2017). Considering that there is substantial interest in monitoring dietary shifts between ^{13}C-distinct resources (Mizutani *et al.* 1992; Sullivan *et al.* 2006; Crowley *et al.* 2013), understanding baseline shifts in $\delta^{13}C$ would be useful for the future application of isotope studies to track resource use in modified systems.

Tracer-isotope analyses

Studies have demonstrated that the pathways of nitrogen uptake and transformation within the soil-plant system are varied (Cameron *et al.* 2013), and thus tracking the cycling of nitrogen poses a complex challenge. The stable isotope of nitrogen (^{15}N) provides a tracer method for study of the inorganic forms of nitrogen and their uptake by aboveground biomass, without the confounding effects of biogeochemical contributions from the soil biota (Barraclough 1991; Pajares & Bohannan 2016). The method which I developed for applying ^{15}N-labelled dung to tropical soils achieved low ^{15}N-enrichment compared to other studies (*e.g.* Nervo *et al.* 2017), but more realistic levels of nitrogen mobility*, i.e.* more thorough incorporation into the dung matrix. Given the expense associated with conventional methods of labelling dung via treatment of forage (Powell *et al.* 2004; Clough *et al.* 2013), further development of my method to achieve high enrichment of truly incorporated material would be an asset to the study of above- and below-ground interactions in the cycling of nitrogen under different land uses.

Conservation application

The ongoing conversion of the tropical landscape (Hansen *et al.* 2013), together with evidence of strong effects of the landscape matrix on biodiversity, necessitates better understanding of ecological changes which take place in remnants of natural forest, both primary and degraded, surrounded by human activity (Ewers *et al.* 2011; Hill *et al.* 2011). Both the configuration and composition of remnant patches can mitigate the absolute impacts of habitat loss on biodiversity and associated ecosystem processes by diminishing fragmentation effects (Kricher 2011; Villard & Metzger 2014). Tropical landscapes, particularly areas of commodity agriculture, are targeted by policies such as those developed for the REDD+ programme, highlighting international awareness of the need to implement educated landscape engineering. The work outlined in this thesis can be developed to explore correlations between predator resource use, and associated food web response, over local and landscape scales to better understand the effect of habitat configuration and composition on ecosystem functioning. Practical assessment of habitat value is essential to prevent misconceptions and delayed collaborations between conservationists and key stakeholders such as logging companies and timber concessions, as has happened previously (Meijaard *et al.* 2006). I have also determined sensitivities of the functional response to both land use and climate change, thus highlighting a much needed tool to study the synergistic effects of these two dominant pressures. In parallel, I have highlighted a novel method to explore the local preservation of ecosystem functioning in agricultural areas, with potential to inform regional and national policy for management of commodity agriculture. Palm oil plantations are increasingly prevalent in tropical landscapes, providing a major challenge to maximise biodiversity, and associated ecosystem functioning, within plantation habitats. The Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme works with the oil palm industry in order to establish the role of biodiversity in tropical agro-ecosystems in order to collaboratively improve the management of oil palm plantation. Safeguarding of biodiversity is likely to preserve local ecosystem functions important for crop production. My work makes a large contribution to the future potential for researchers to meet the challenge to demonstrate that relationship empirically.

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